AN EXPERIMENTAL EXAMINATION

OF THE

ANTI-PREDATOR RESPONSE

IN THE

MONGOLIAN GERBIL

(MERIONES UNGUICULATUS)

A Thesis

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by

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ABSTRACT

This study was conducted to examine the hypotheses that (a) an anti-predator response occurs in the gerbil to a visual stimulus, (b) differences in responsiveness occur for the gerbil to short and long-necked stimuli and (c) stimulus specific response decrement occurs for the anti-predator response in the gerbil.

Three groups of gerbils were used. After one day of free movement, two experimental groups were presented with short and long necked stimuli, respectively, for five days and counter-balanced with the opposite stimulus for one-half of the eight presentations on the seventh day. The dependent measures recorded observationally were the startle and anti-predator responses, ambulation, time out of the field, territorial marking, grooming and digging.

The results support the occurrence and habituation of the anti-predator response, and the ancillary startle response, while not showing overall differences in responsiveness to the short or long-necked stimuli and only partial stimulus-specific response decrement. Initial high rates of startle and anti-predator responses did occur with increased time in the enclosure and suppression of ongoing behaviors as ambulation, territorial marking, grooming and digging.

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CHAPTER I

INTRODUCTION

Statement of the Problem

The purpose of this thesis was to examine experimentally the Mongolian gerbil, Meriones unguiculatus, for (1) the occurrence of the anti-predator response to a visual stimulus; (2) the possible differences in frequency of responses between presentations of short-necked stimuli (hawk shape) and long-necked stimuli (goose shape); and (3) whether or not stimulus specific response decrement occurs with the anti-predator response.

The anti-predator response in the Mongolian gerbil derived from the ecological study made by Tanimoto (1943) and preliminary laboratory observations by the present writer. Tanimoto notes the gerbil as having a underground burrow complex with many entrances used to escape predators. A photograph of the Mongolian gerbil's natural habitat given by Tanimoto shows the openness of the terrain that leaves the burrow as the only place of refuge from predation (see Figure 1). Unfortunately no mention was made of the type of predator as it could be avian, reptilian or mammalian (Kirmiz, 1962). With this information preliminary laboratory observations by the present writer indicated that some fast moving stimuli elicited startles and escape-from-the-open-field responses when a "burrow" exit was provided. Repeated presentations of the stimuli elicited repeated "anti-predator" responses.
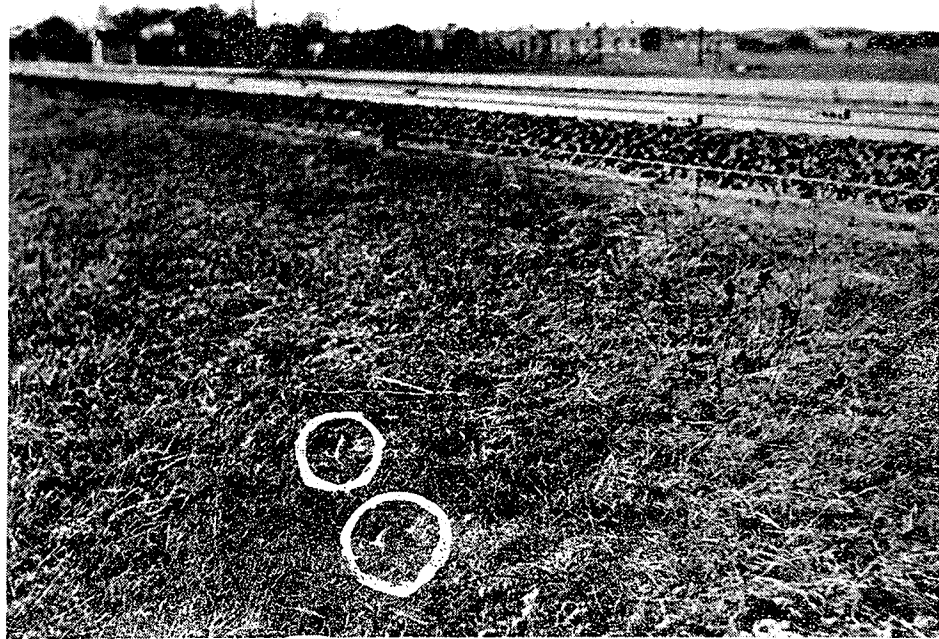
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FIGURE I

The Gerbil's Natural Habitat

History of the Problem

The history of a paradigm for the anti-predator response to aerial predators has been traced back to the 19th century lawyer and experimental behaviorist Douglas A. Spalding by Gray (1966). Modern research on the subject was centered around a hypothesis put forth by Tinbergen (1948; 1951). The hypothesis suggested that "gallinaceous birds, ducks, and geese" exhibit innate alarm reactions to short-necked, long-bodied (hawk shape) stimuli resembling predators and no reactions to long-necked, short-bodied (goose shape) stimuli.

The controversy that followed Tinbergen's publications was initiated by a test of the hypothesis using White Leghorn checkens by Hirsch, Lindley, and Tolman (1955). This study failed to confirm the Tinbergen hypothesis, as it was called by Hirsch et al. under laboratory conditions. A second experiment by Rockett (1955) corroborated these results with White Rock checkens and ducks. Tinbergen (1957) criticized the Hirsch team for having based their negative findings on tests of another species that was domesticated and noted that valid criticisms, such as giving only summarily published observations and having the developmental history uncontrolled, were not mentioned. Hirsch (1957) replied that it was correct to use domesticated Leghorn chickens as they were the most available gallinaceous birds for which the hypothesis was framed. Tinbergen never gave a direct answer to Hirsch's reply.

The controversy over the Tinbergen hypothesis gave impetus to several more experiments. Melzack, Penick, and Beckett (1959) used moving "hawk" and "goose" figures to test differential responsiveness by Mallard ducks, some of which received earlier experience with the stimuli. Mallards with early experience showed no responses to later testing, whereas, birds with no early experience showed marked fear of both the "hawk" and "goose" shaped models. Both in this study, and in a second study by Melzack (1961), habituation to successive presentations occurred, although even after two thousand presentations of the models "non-emotional" orienting responses were found. At approximately the same time, McNiven (1960) found, in a study of New Hampshire chickens, Mallard ducklings and unspecified young pheasants, that there were no differences in responsiveness to the "hawk-goose" variable. McNiven did find that all three species exhibited escape responses to both the "hawk" and "goose" shapes when they were presented swooping.

These researches and criticisms had their effect on Tinbergen. First in a 1963 publication, and then more extensively in a 1965 publication, Tinbergen (1963; 1965, p. 130) repealed his earlier commitment to the difference in responsiveness to the short-necked and long-necked figures as having an innate basis. A new position was outlined crediting habituation to familiar, non-predatory, goose-like species as being the basis of the difference in reactivity to unfamiliar predators. Accordingly, Tinbergen

(1965) argued that early in development there is a generalized, non-specific reactivity to moving objects which declines with the increasing frequency of their occurrence. Those new, or strange stimuli, such as predators, still elicit reactions because habituation has not taken place. Thus, Tinbergen, the major advocate of the original hypothesis based on innate schemata, accepts what were the findings of Schleidt (1961a; 1961b). Schleidt (1961a) found that stimulus specific response decrement occurred with turkey hens to more frequent stimuli, hawk-like or goose-like. Since predators are a relative rarity, in comparison with non-predators, they would still elicit reactions. Agreeing with Schleidt, Marler & Hamilton (1966) note, "thus habituation serves to achieve one of the most striking cases of response to a specific stimulus that has been demonstrated (p. 647)."

The possible importance of habituation as an ontogenetic adaptation to biologically irrelevant stimuli is apparent and accepted (Lorenz, 1965; Thorpe, 1965; Marler & Hamilton, 1966). As a simple learning process, habituation permits response decrement to innocuous stimuli. Although at first a simple conception, habituation is complicated by the possibility of being short-term or long-term, specific to the stimulus or not specific to the stimulus and being confused with sensory adaptation (Thorpe, 1965). Thorpe speaks of habituation "in the strict sense" as refering to long-term response waning specific to a stimulus, but uses the term for "the waning of a response as a result of repeated stimulation that is not followed by any kind

of reinforcement. (Thorpe, 1965, p. 487)."

History of the Species

The term gerbil can refer to any species of the ten genera of the sub-family Gerbillinae, of the family Cricetidae, sub-order Myomorpha, of the order Rodentia (Simpsom, 1945; Schwentker, 1968). In the present context the name gerbil will refer to only the Mongolian gerbil, Meriones unguiculatus, first identified by Milne Edwards in 1867, who reported on it in a French journal after the missionary Armond David sent gerbil skins and skulls to Paris. It is native of Northeast China, Eastern Mongolia and parts of Korea and was brought, indirectly via Japan, into North America. Victor Schwentker of the West Foundation in New York State introduced eleven pairs of gerbils, nine of which bred beginning in 1954. Most, if not all, of the presently used research animals have descended from this small sample breeding stock.

The small sample raises the question of whether the now available gerbil is representative of the free living form. Several phenomena are pertinant. First such a small sample used for the establishment of a new population can carry only a small partitioned proportion of the total genetic load of the parental population (Mayr, 1963, p. 211). The descendant population contains only the relatively few genes that the founders had brought with them, until replenished by subsequent mutant alleles. This "founder principle," as it is called by Mayr (1963), is often responsible for the genetic and phenotypic

uniformity of animal colonies; a generalization which may well apply to the West Foundation stock. Schwentker (personal communication, 1969) notes that there is no access to wild gerbils for comparison. For the present then there is no way of testing the effects that the founders had on representativeness. Secondary variables in representativeness include the epigenetic consequences of the domesticate's ontogeny noted by Spurway (1955), the transition Hale (1962) emphasized between the two adaptive peaks that gene frequencies undergo in adapting from the wild to domestic state, and genetic variation within genetically isolated populations. The question of representativeness of the available gerbil will not be resolved until the parental population is resampled under standardized conditions for comparison. There seems to be universal agreement that ecological data is particularly sparse on the gerbil (Thiessen, 1968a; Schwentker, 1963).

The majority of the available behavioral studies on the gerbil have been done recently. Twenty-six of the thirty available have been done within the last three years. The first study was by Tanimoto (1943), which included behavioral observations and remains the only extensive source of ecological data on the gerbil. Gerbils were reported to live in underground colonies and construct complexes of burrows, nests and storerooms in dry, sandy soil. The burrows are approximately cylinderical with about a 4 cm. diameter and are used to escape predators. Tanimoto (1943) makes no reference to the type of predator, and, if desert fauna from other parts of the world are

similar, it may be a bird, reptile or mammal (Kirmiz, 1962). A photograph (Figure 1) taken from Tanimoto (1943) is of the gerbil's native habitat in Northern China. Two circles in the photograph enclose gerbils that he observed. The habitat can be seen to be open, flat and free of ground cover, leaving the burrows as the only escape route from predators. In relationship to the anti-predator response "foot-stomping" may have a communicatory function in the gerbil, as Kirmiz (1962) suggests in the jerboa, Fraculus orientalis. In the case of the gerbil it may function as an alarm signal to the presence of the predator outside of the burrow as in some cases foot-stomping occurs after the presentation of a predator stimulus and may heighten the reactivity of conspecifics (personal observation). Clearly this possibility is speculative and requires field study. In addition to this occurrence, foot-stomping has been noted to occur regularly during copulatory sequences and male-female encounters by Routtenberg & Kramis (1967).

Territorial marking in the gerbil has been extensively studied by a group at the University of Texas led by D. D. Thiessen. It is important to quality the use of the concept of territory as Tanimoto (1943) makes no mention of it in regard to gerbils. Territory, defined by Noble (1939) as "any defended area," would be one of the many possible functions of intraspecific chemical stimuli among which are aggregation, dispersion, individual and group recognition, trail laying, as well as sexual and alarm signals (Marler & Hamilton, 1966). Evidence for the use of pheromones as territorial signals

is suggested in the findings of Blum & Thiessen (1968) that gerbils exposed to open fields marked by other gerbils are more hesitant to explore them. Pheromones may be found to have multiple social functions in the gerbil and, according to Thiessen (1968c), will have to remain a "laboratory curiosity" until their social significance is well defined.

Marking in the gerbil is characterized by skimming prominent features of their environment with the midventral sebaceous gland leaving sebum, which is oily to touch and musky in odor. The male's gland-field on the ventral epidermis is about twice the size of the female's and both sexes prefer to makr objects that are high, relatively long and smooth on the surface, according to Thiessen (1968a; 1968c). Circadian entrainment is found for the marking response which tends to be more nocturnal and particularly high around dawn and dusk. Open fields premarked by conspecifics decreases marking, defecation and urination, particularly in the male. Sex differences were also found to occur in the frequency of the response, males marking twice as many times as females after being adapted to the field (Thiessen, 1968a; 1968c). By castration and reinstatement with testosterone propionate, marking was shown to be androgen dependent in both sexes (Thiessen, 1968a; 1968b; Lindzey, Thiessen, Tucker, 1968; Thiessen, Friend, Lindzey, 1968).

The evolutionary origins of territorial marking and "sand-bathing" are inextricably tied, according to Eisenberg (1967), due to their similar topography.

Sandbathing is a behavior shared by all desert-adapted rodents permitting the pelage to be dressed without water. In the general case, sandbathing consists of several distinct movements, including side rubbing, ventrum rubbing, writhing from side to side, and rolling on the back. The organization of the response is species-specific and in the gerbil consists of side rub to opposite side rub in a ritualized form (Eisenberg, 1967). Since only side rubbing is characteristic of sandbathing in the gerbil it is easily differentiated from marking, which is characteristically ventrum rubbing.

The other behavioral studies that have been done using the gerbil are lacking in ethological data. These studies, and other studies noted in this section, are summarized in Table 1. Generally they show the gerbil to be admirably docile and applicable to many forms of psychological instrumentation and methodology, such as wheel running, Sidman avoidance, shuttlebox avoidance, maze studies, operant conditioning studies, jumping stands, visual cliffs and open fields. Gerbils are poorer in visual cliff discrimination than rats or mice, although their performance can be improved with adolescent experience. The gerbil is social and has a variety of interesting behavior patterns yet to be explored in any depth, such as shredding, spontaneous seizures, and sand digging.

The laboratory maintenance required for the gerbil, of all rodents, is perhaps the least demanding. Gerbils are easily kept and handled, requiring little water and only standard laboratory chow. The gerbil's high activity,

odorlessness, ease in handling, durability, as well as its fit to standard psychological paradigms, predict its increased usage in behavioral research.

In addition to the docility of the gerbil its species specific behaviors make it a particularly worthwhile laboratory subject. The status of the "comparative" nature of animal studies in psychology has been seriously questioned as lacking a theoretical basis in evolutionary biology (Lorenz, 1950; Beach, 1950; Schnierla, 1952; Lockard, 1968; Driver & Corning, 1968; Hodos & Campbell, 1969). The gerbil used in comparative ethological studies, as for example the emphasis on the evolution of social behavior in rodents by Eisenberg (1967), may contribute to the tempering of these admonishments.

Table 1

Summary of behavioral studies with the Mongolian Gerbil
(Meriones unguiculatus)

Behavior	Reference
Males mark territories with sebaceous gland more than females. Animals exposed to marked fields more hesitant.	Blum & Thiessen, 1968
Mice better gerbils which better kangeroo rats in shuttlebox avoidance.	Boice, Boice & Dunham, 1968
Operant responses for food on FR 1 and VI 1-min. are slower in rate than rat or pigeon.	Campbell, Straney & Neuringer, 1969
Within limits depth and distance perception present in jumping stand and T-maze apparatus.	Cole & Topping, 1969
Visual and tactile cues regulate cliff descent responses.	Collins, Lindzey & Thiessen, 1969
Gerbils better rats in two-way active avoidance in shuttle box.	Eggleston, 1967
"Sandbathing" and area marking; sociable; several mounts, intromissions in copulatory sequence.	Eisenberg, 1967
Time "paper shredding" increases with thickness of paper.	Glickman, Fried & Morrison, 1967
Hippocampal lesions increases motor activity and decreases neophobic responses.	Higgens, Glickman & Isaacson, 1967
Hippocampectomized gerbils show enhanced reactivity to high intensity auditory & visual stimuli.	Ireland & Isaacson, 1968
Learning sets establish for two and four choice object discrimination in WGTA.	King, Goodman & Rees, 1968

Table 1   con't

Development of territorial marking in male gerbil androgen dependent.	Lindzey, Thiessen & Tucker, 1968 [13]
Excised sebaceous gland didn't prevent reproductive success.	Mitchell, 1967
Gerbil appropriate subject for Skinner box, discrimination runway and open field study.	Nauman, 1963a, 1963b
Gerbils less thigmotaxic than rats.	Nauman, 1968
More active than rat in running wheel; comparable to rat in Sidman avoidance.	Powell & Peck, 1969
Self-stimulation of brain, sexual behavior and foot shock are followed by "foot stomping."	Routtenberg & Kramis, 1967
Scopolamine disrupts paper chewing; no effect on spontaneous activity.	Stitzer & Issaacson, 1968
Live together in undergound colonies; have many burrows to escape their predators.	Tanimoto, 1943
Androgen dependent marking decreases with grouping.	Thiessen, 1968a
Testosterone induces marking and sebum secretion in female.	Thiessen, 1968b
Territorial marking reviewed noting that the hormone-behavior relation is probably of social significance.	Thiessen, 1968c
Castration and testosterone replacement show androgen control of marking which is probably a pheromone.	Thiessen, Friend & Lindzey, 1968
Visual cliff behavior deficient but not brightness discrimination.	Thiessen, Lindzey, Blum, Tucker & Friend, 1968
Early experience with visual cliff decreases latency to respond.	Thiessen, Lindzey & Collins, 1968
Spontaneous seizures controlled by anticonvulsants; genetic variability.	Thiessen, Lindzey & Friend, 1968
Odor cues effect goal latency in runway.	Topping & Cole, 1969
Shock avoidance better than rat.	Walters, Pearl & Rogers, 1963
Blind and vibrissaeless gerbils poor in maze learning.	Webster & Caccavale, 1966
Gerbil discrimination poorer than rat.	Wise & Parker, 1968

CHAPTER II

METHOD

Subjects

Twenty-seven Mongolian gerbils, <u>Meriones unguiculatus</u>, were received

from the supplier Victor Schwentker of Tumblebrook Farms, Inc. at the age

of 56 days. Paired heterosexually, the 13 males and 14 females, one female

of which was placed with a previously acquired male, were put into specially

constructed 14 x 14 x 8 inch, wire mesh topped, masonite cages painted

semi-gloss white on all six sides (see Figure 2). Purina Lab Chow was

always available through a wire mesh feeder, as was water, in one side of

the cage. The cages were cleaned once a week and the floor's $\frac{1}{4}$ inch sawdust

substrate was replaced. Pairs that had young were given paper as nesting

material and the pups were removed at 30 days of age.

The gerbils were maintained on a twelve to nine A.M. dark, nine to

twelve light cycle in a isolated room in which only limited movement by a

caretaker was permitted and no other animals were kept. Approximately

80 db. of white noise was played continuously during the light portion of the

day-night cycle in both the colony and experimental rooms to mask environ-

mental noises and increase circadian cues. The gerbils were approximately

180 days old at initial testing.

Apparatus

The apparatus consisted of a 39.7 inch square open field with a grid of

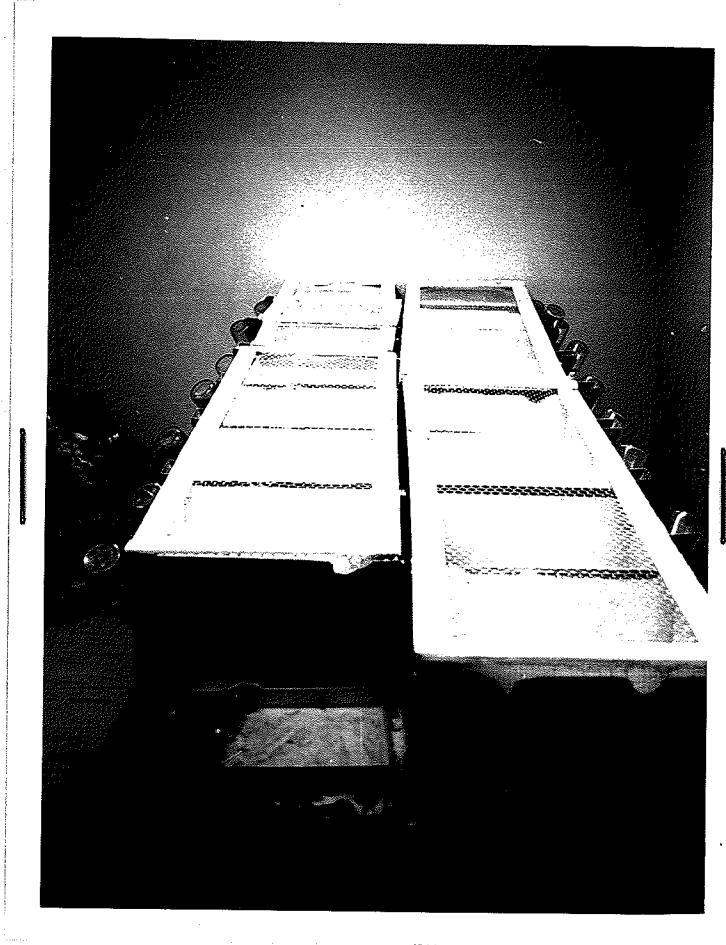16 equally-sized squares drawn in black of a white semi-gloss floor. The

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FIGURE 2

Cages in Room of Gerbil Colony

field was studded with nine frosted Plexiglas pegs measuring 1.0 inch in length, 7/16 inch in width, and 9/32 inches in height, after Thiessen (1968c). Each peg was positioned for use as a territorial marking site at each of the nine intersecting points of the grid. Three of the 4 x 4 feet, white, semi-glossed, masonite sides to the open field met with the fourth wall that was fourteen inches high and consisted of first 8.5 inches of white masonite topped by 5.5 inches of clear Plexiglas. The Plexiglas top permitted the predator stimulus to be viewed from the opposite 75% of the field. Eight inches in the back of the fourth wall a white, semi-glossed, 4 x 4 feet cardboard partition provided a blind for the predator stimulus launching apparatus and the observer. The predator stimulus moved through a $2\frac{1}{2}$ x 16 inch horizontal slot 18 inches from the floor base of the blind and the observer had a $2\frac{1}{2}$ x $7\frac{1}{2}$ inch horizontal slot adjacent to the launching apparatus in the blind. A darkened room and a light over the open field permitted only limited acuity by the gerbils through the blind.

The predator stimulus was a reversable, black, long-necked or short-necked form shown in the lower photograph of Figure 4, after Schleidt (1961b). The stimulus was 14 inches wide by 12 inches long and moved on the end of a five foot long by 3/4 inch square, white pole so that it could move horizontally 18 inches off the floor to the opposite side of the open field, coming to a halt over the opening of the enclosure. The power for the stimulus launching
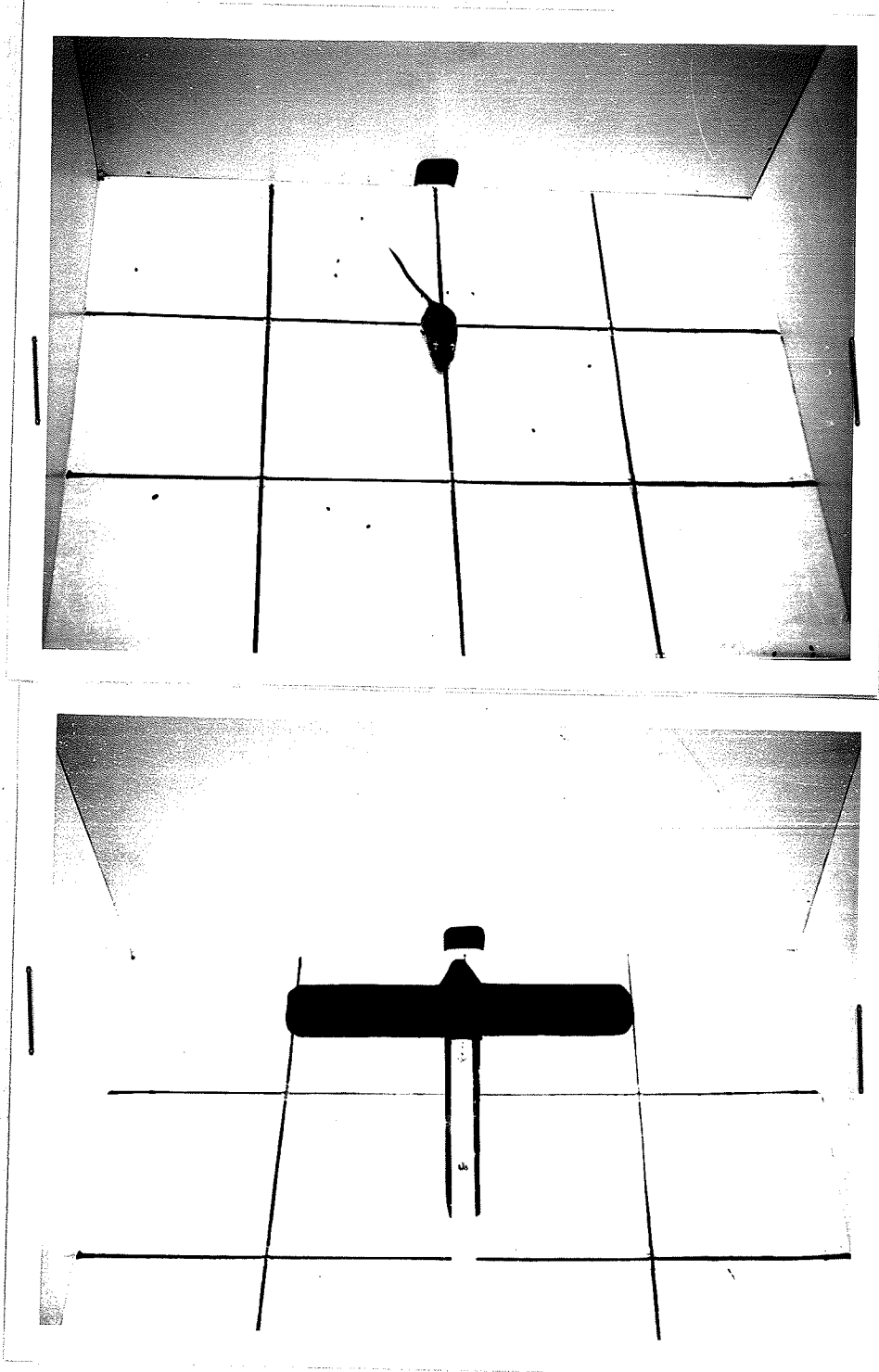
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FIGURE 3

Gerbil in field and Hawk-like Stimulus

apparatus consisted of a Variac operated, 1/6 h.p., reversable A.C. motor

connected via two pulleys and rope sets to a sliding track on which the predator

stimulus slid. From the observer's seat the control box for the launching

apparatus permitted ejection of the stimulus into the open field at a fixed

rate of 4 ft./sec. with a reduced recall spped.

In the center, at the base of the wall opposite the entrance for the predator

stimulus, a six inch long by two and 1/2 inch square "burrow" enclosure was

placed. This enclosed area consisted of only one percent of the total apparatus

area open to the gerbils and had white flooring with black top and sides. It

was removable from the side of the open field to permit the entrance and exit

of the subjects.

A Cramer type 633s-AO8-E electric timer was tied to a Hunter model

140A counter, both of which permitted the recording of the time spent out

of the open field and the number of exits from it. A Sodeco electric counter

was used to record the number of lines crossed in the observation periods of

each 20 minute session. The entire 20 minute session was timed by a stop

watch.

Procedure

The gerbils were moved in a sealed container from the colony room, in

a fixed time interval to control for possible differences in arousal due to time

in transport, to the room where the experimentation was being carried out.

The gerbils were always handled by the base of the tail and were placed in

the apparatus at the enclosure connected to the open field, as the gerbil

shown in Figure 4. At this point the total time clock was begun which would

schedule the 20 minute exposure to the open field. The open field and

enclosure were washed with a mild soap solution after each 20 minute session

removing hair, feces, urine and sebum.

Three groups of nine gerbils matched for sex, as far as possible, and

randomly distributed were exposed to the open field one at a time, for 20

minutes per day, for seven consecutive days. The first day of exposure to

the field all animals were permitted to move freely and explore their new

environment while being observed. No presentation of the predator stimulus

was made to any of the three groups on the first day.

The frequency of and temporal distribution of various behaviors in

minute blocks were recorded on the data sheet (see appendix). With the

exceptions of territorial marking and line crossing, these behaviors were

scored as having occurred, or not occurred, in each minute block. The

frequency of territorial marking was the only behavior for which each

occurrence per minute block was scored. The frequency of line crossing

was summed for the entire 20 minute session and each crossing was counted

without breaking visual contact with the subject. Observations were time

sampled from the first 50 seconds of each minute block and recorded in the

remaining ten seconds. The behavioral classes included digging, a rapid

movement of the forepaws against an object; washing, a care of the body

surface with the mouth; forepaw wipe, a care of the body surface by sweeping the forepaws over the pelage; scratching, a care of the body surface by hindpaw movement of the pelage; sandbathing, a care of the body surface by rubbing one side then the opposite side to the floor; upright, a bipedal standing position; testing the air, a bipedal standing position with a sniffing of the air; gnawing, an engagement of the teeth with an object; defecation and urination. The amount of observed time that was spent out of the field and the number of exits from it were recorded on the clock and counter over the entire 20 minute session. The number of line crossings was also recorded over the entire 20 minute session. The interest in taking the basal observations was to have data with which to make group comparisons whose relationships were apparent.

The second day of experimentation four male and five female gerbils in Hawk-like Stimulus Group (A) received eight presentations of the short-necked stimulus during the last 15 minutes of the 20 minute session. Both the startle response and anti-predator response were scored as having occurred, or not occurred,for each presentation on the data sheet. The startle response was defined as immediate rapid flight and orientation from the stimulus source. The anti-predator response was defined as leaving the open field within ten seconds of the launching of the stimulus while the anterior of the animal faced the stimulus source at less than 90° from its sagittal plane in the opposite 75% of the open field. The stimulus was only presented while the

subject was still and the response was scored as occurred, or not occurred, on the data sheet. This procedure was followed from the second to the sixth day in group A with the stimulus being withdrawn immediately after presentation. On the seventh day the stimulus was reversed, for the first four of eight presentations, to the long-necked stimulus. The identical procedure was followed for Goose-like Stimulus Group (B) except that its four males and five females received the long-necked stimulus for days two to six and counter-balanced on the seventh day, receiving four short-necked and four long-necked stimulus presentations. In this manner both experimental groups received the same procedure with the exception of having the opposite stimuli.

The five males and four females of group C acted as a control group in that no visual stimuli were presented on days two to seven. Basal observations were made during this period for comparisons with experimental groups.

CHAPTER III

RESULTS

Scores were taken from each of the seven data sheets per gerbil and tabulated for the following dependent measures: ambulation, startle response frequency, anti-predator response frequency, time observed in enclosure, territorial marking frequency, the frequency of 50 second time samples in which forepaw wiping and washing as well as digging occurred. Means were calculated for plotting and appropriate non-parametric statistical analyses were carried out as suggested by Siegel (1956). The data are reviewed to contrast first the experimental groups with the control group, second the Hawk-like Stimulus Groups (A) with the Goose-like Stimulus Group (B) and third the effects of counter-balancing on the last day with a new stimulus. Figures show mean occurrence of the behaviors of all animals on each day.

The frequency of occurrence of the startle and anti-predator responses for the two experimental groups and the one control group is shown in Figure 4. Neither the startle nor the anti-predator response occurred during the observation periods in the one control group. Both the occurrence of the startle and the anti-predator responses in the experimental groups contrasted with the control group over days two to seven is statistically significant according to the Wilcoxon Matched Pairs Test (T = O, P < 0.01, 2-tailed).

The number of line crossings as an index of ambulation for the three groups is shown in Figure 5. The difference in ambulation between Hawk-like

Stimulus Group (A) and the control group is significant on day two, the first day of stimulus presentation (T = 4, P<0.05, 2-tailed). The same was the case for the difference in ambulation between Goose-like Stimulus Group (B) and the control group (T = O, P< 0.01, 2-tailed). From day two to day three an increase in ambulation occurred for both experimental groups and a corresponding decrease for the control group to a point at which there was no significant differences between them on the third day (P>0.05).

The time spent out of the open field and in the enclosure is shown in Figure 6. An increase in the amount of time spent out of the open field is shown in the two experimental groups although it does not in either case meet significance. The drop in time spent in the enclosure from day two to day three in the Hawk-like Stimulus Group (A) is significant with a T of four (P< 0.05, 2-tailed). The decrement in time spent out of the open field in group B from day three to day four is also significant (T = 4, P < 0.05, 2-tailed). An interesting sex difference was found for the time spent in the enclosure in both experimental groups. In each of the two groups, in which 48 stimulus presentations were given over the last six days, females spent significantly more time in the enclosure than males (see Table 2). In the control group the relationship was somewhat reversed with the females spending more time in the field than males, although this difference was not significant.

Territorial marking was another dependent measure that declined in

occurrence in the two experimental groups after the onset of the stimulus presentation. The differences shown in Figure 7 between the males in the Hawk-like Stimulus Group (A) and the Control Group (C) on days two and three are significant according to the Mann-Whitney U Test (U = O, $P < 0.014$). The males in Goose-like Stimulus Group (B) were only significantly different from the Control Group (C) on day three (U = O, $P < 0.014$). Overall sex differences were apparent with males marking 13.7 times more than females; a finding consistent with the reports of sex differences by Thiessen (1968a).

Other behaviors whose changes in frequency coincide in the experimental groups with the onset of the stimulus presentation on the second day are digging and the two forms of grooming pooled under one score, the forepaw wipe and the body wash. As shown in Figure 8 the number of 50 second time periods in which digging was observed increased from day one to day two in the control group and decreased in the experimental groups. The differences, however, were only significant between the Goose-like Stimulus Group (B) and the Control Group (C) on days two and three (T = 3, $P < 0.02$; T = 4.5, $P < 0.05$ respectively). Overall it would be conservative to say that 75 percent of the digging occurred in the enclosure, i.e. one percent of the total area open to the gerbils.

A sharp increase in the frequency of 50 second time samples in which forepaw wiping and washing occurred in the control group, as shown in Figure

9, with a corresponding decrease from day one to day two in both experimental groups. The Hawk-like Stimulus Group (A) was significantly lower in fore-paw wiping and washing on day two although not on day three (T = 0, P< 0.01). The Goose-like Stimulus Group (B) had significantly fewer wipes and washes compared to the control group on day two and three (T = 3, P< 0.02; T = 4, P< 0.05 respectively). Body washing is a more extensive and less frequently occurring form of grooming compared with the forepaw wipe. Washing some-times occurred in the anal region after defecation and at times included separation of the pelage with the forepaws followed by mouthing characteristic of the behavioral sequence. The forepaw wipe ranges from brief anterial sweeps of the dorsal pelage to extended and repeated sweeps at times leaving the pelage standing on end in a crest-like fashion.

The startle response is topographically similar to the anti-predator response, the latter not occurring with the absence of the former. In some cases skidding flight toward the enclosure from the sides of the field resulted in the gerbil overshooting the entrance due to poor traction and after remaining in the field. The essential difference as defined in this study is that after head lowering and orientation from the stimulus flight consummated in entrance to the enclosure in the case of the anti-predator response. Figure 4 shows that on days two and three startle responses occurred more frequently for Hawk-like Stimulus Group (A) than for Goose-like Stimulus Group (B). The relation-ship is reversed for the next three days with more rapid startle response

decrement occurring in group A. The anti-predator response occurred more frequently in the Goose-like Stimulus Group from day two to day six when compared with group A. To test the anti-predator response between groups A and B two non-parametric tests, the Wilcoxon Matched Pairs and the Friedman Two-way Analysis of Variance, and the parametric test, the F test, failed to show significance for days two to six. Differences between subjects scores in group A and B for days three and four were significant according to the Wilcoxon with a T of 3.5 ($P < 0.05$, 2-tailed). Ambulation was higher for Hawk-like Stimulus Group (A) on day three than for Goose-like Stimulus Group (B), the same day the frequency of the anti-predator response dropped significantly in group A (see Figures 4 & 5). Females tended to be more reactive as measured by the frequency of startle and anti-predator res- ponses, but for neither group A nor B were sex differences significant on these measures.

Counter-balancing on the seventh day by presenting the goose-shaped stimulus for the first four trials in Hawk-like Stimulus Group (A) and the hawk-shaped stimulus for the first four trials in Goose-like Stimulus Group (B) resulted in differences between groups in responsibility as shown in Figure 4. Group A made a significant increase in startle responses from day six to day seven as well as significantly more responses for the new goose-shaped stimulus on the first four trials of day seven ($T = 0$, $P < 0.05$; $T = 0$, $P < 0.01$ respectively). Neither the startle response in group B nor the anti-predator responses in groups A and B showed increases for the counter-balancing on

day seven that were significant, although all anti-predator responses in both groups occurred to the counter-balanced stimulus. The time spent in the enclosure on the counter-balanced day for group A increased considerably (Figure 6), and the frequency of forepaw wipes and body washes decreased, the latter of which was significantly different from controls on day seven ($T = 0$, $P < 0.01$).

After startle and anti-predator responses ceased occurring changes in behavior upon presentation of the stimulus were still most often noticeable, although in some cases subjects did not respond with the most elementary head orientation. Approach responses from a standing position in the direction of the stimulus entrance window followed by orientation towards the window in the upright position were common. In some cases an extended upright position and "testing the air" occurred while oriented towards the stimulus entrance consummating the approach sequence.

TABLE 2

Mean Time in the Enclosure
per Daily Session

Groups	Male	Female
Group A*	114.4	173.5
Group B**	98.0	206.6
Group C	124.9	84.0

* significant sex difference ($U = 3$, $P < 0.056$)
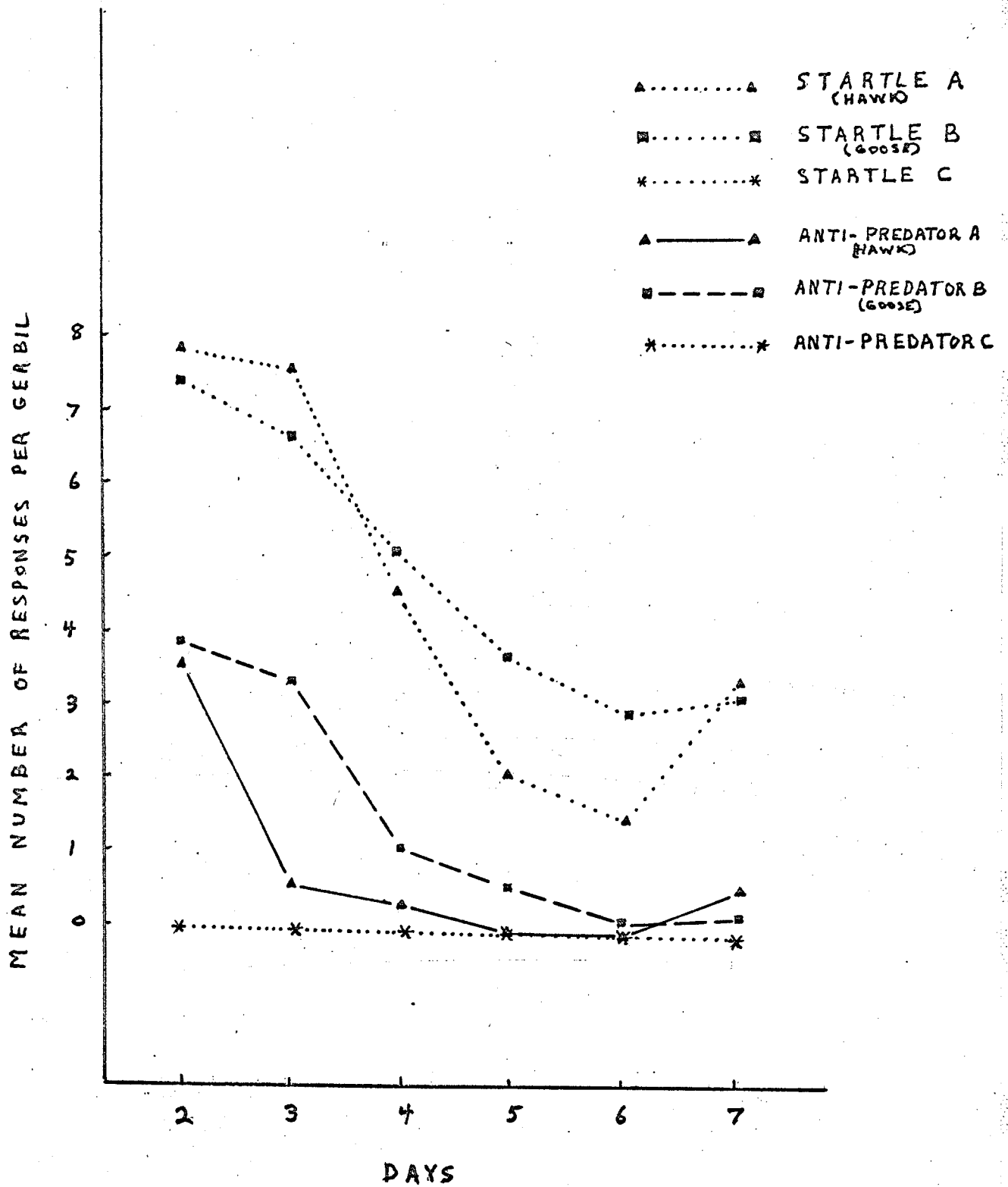** significant sex difference ($U = 2$, $P < 0.032$)
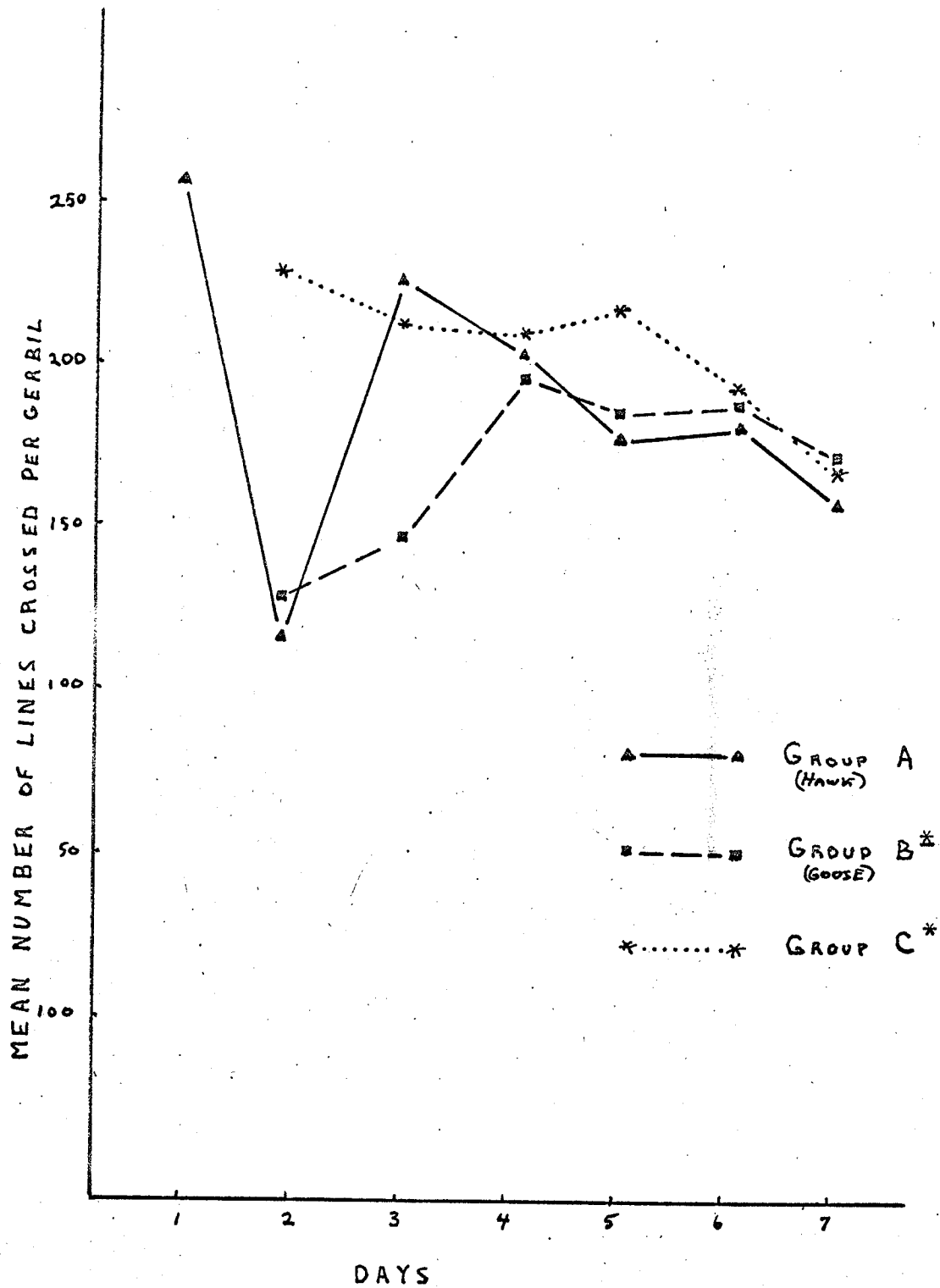
FIGURE 4

RESPONSE DECREMENT OVER DAYS

FIGURE 5

ACTIVITY LEVEL OVER DAYS
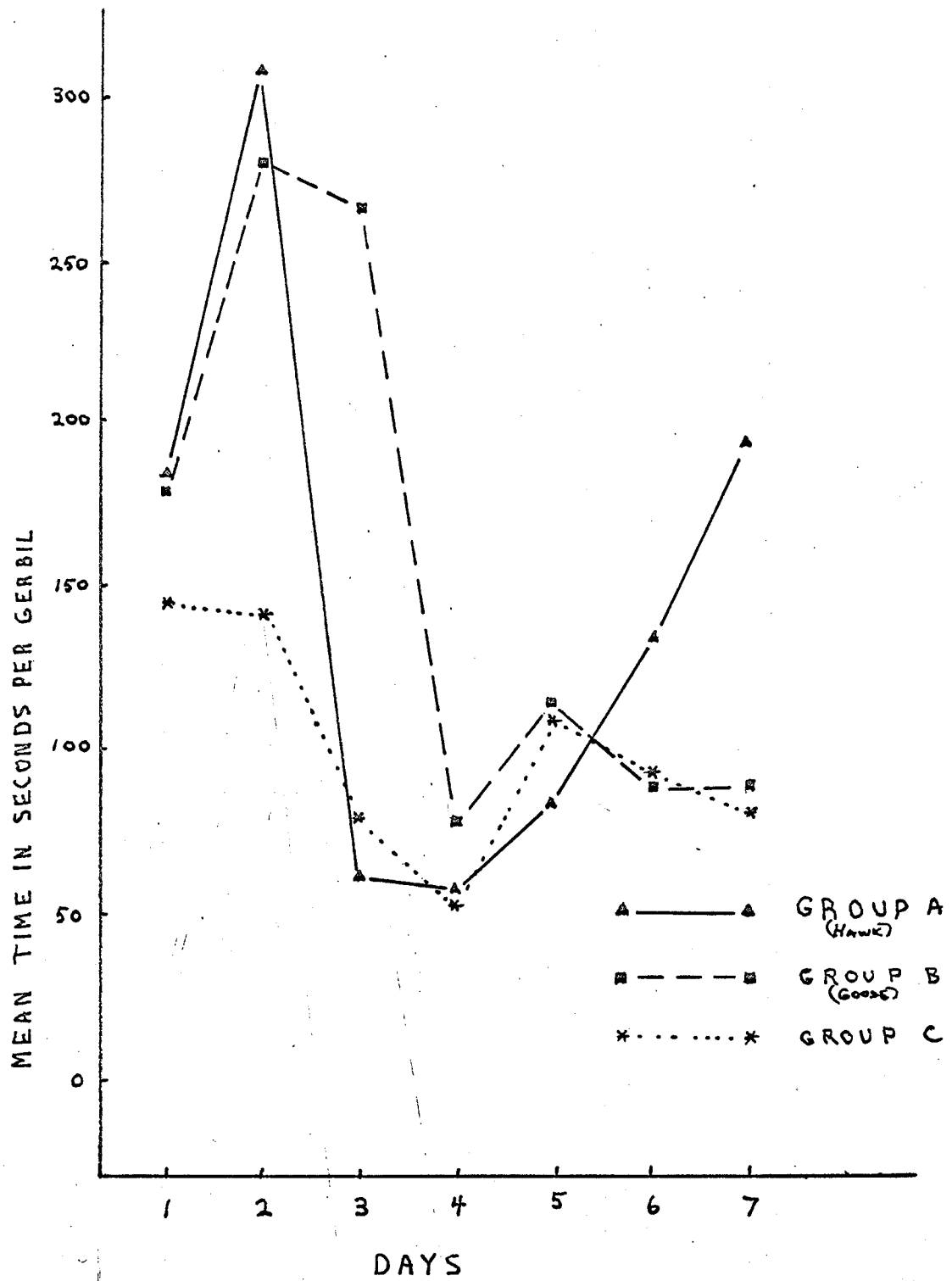
* Data not available for day 1.

FIGURE 6

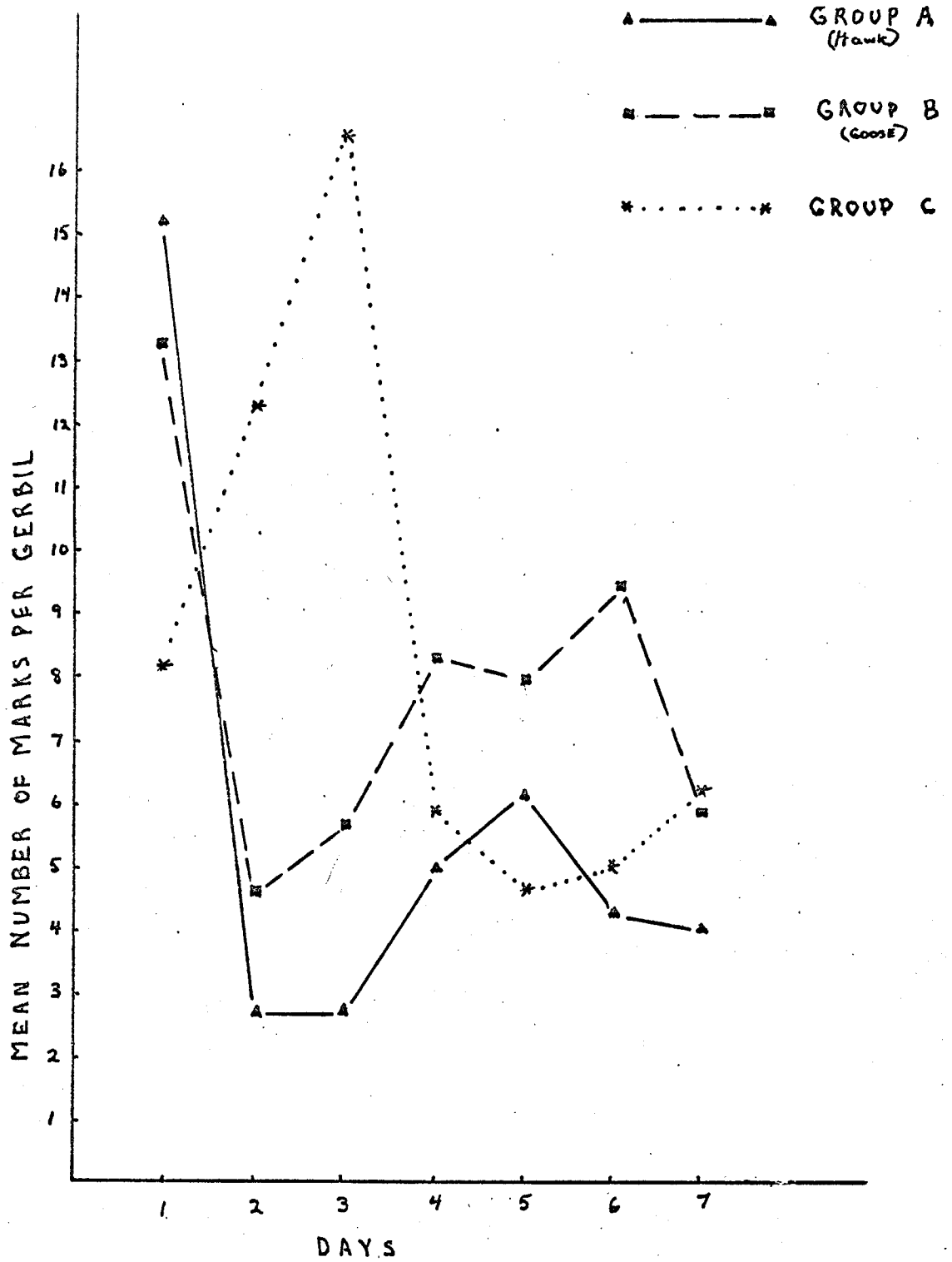TIME SPENT OUT OF OPEN FIELD IN ENCLOSURE
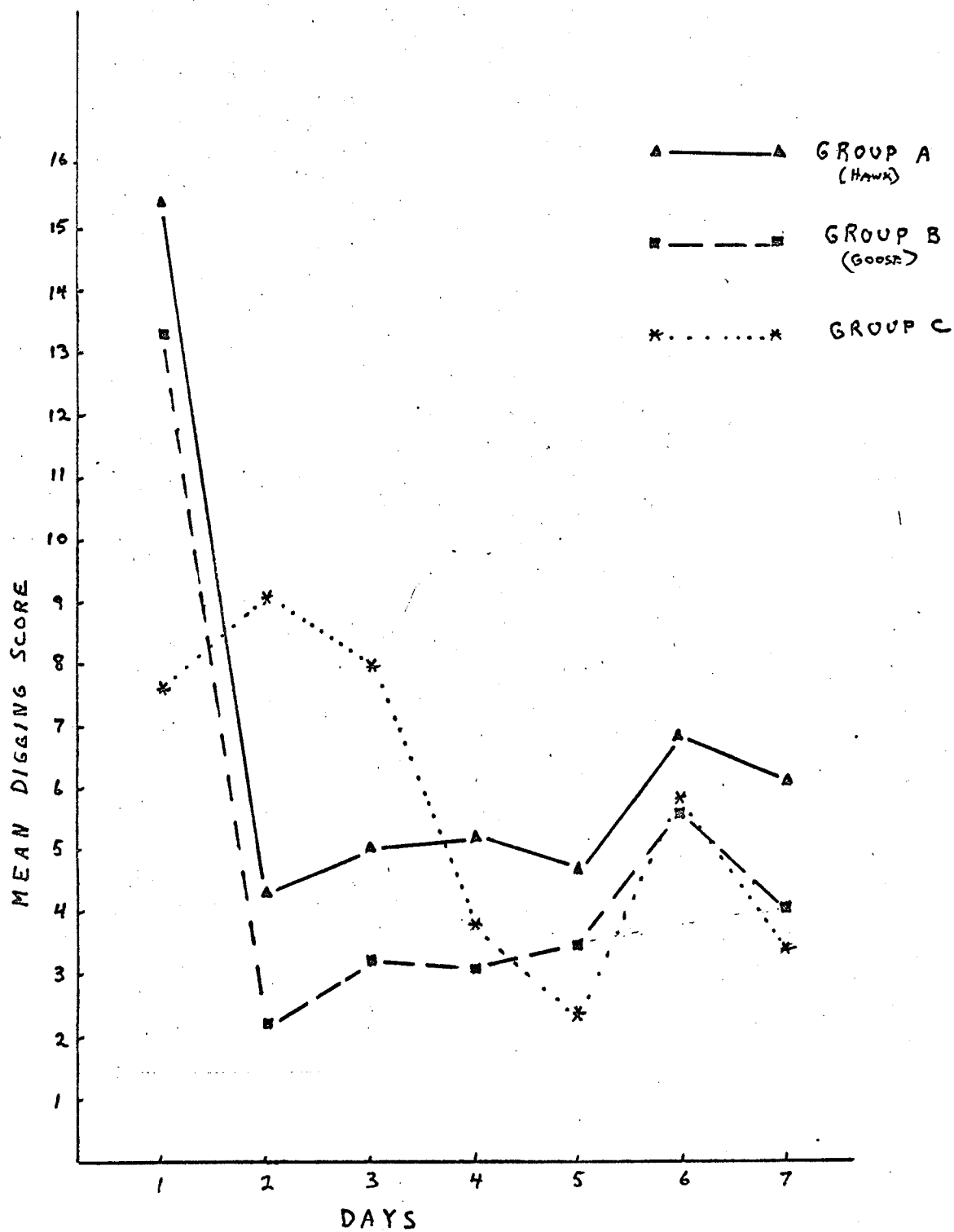
FIGURE 7

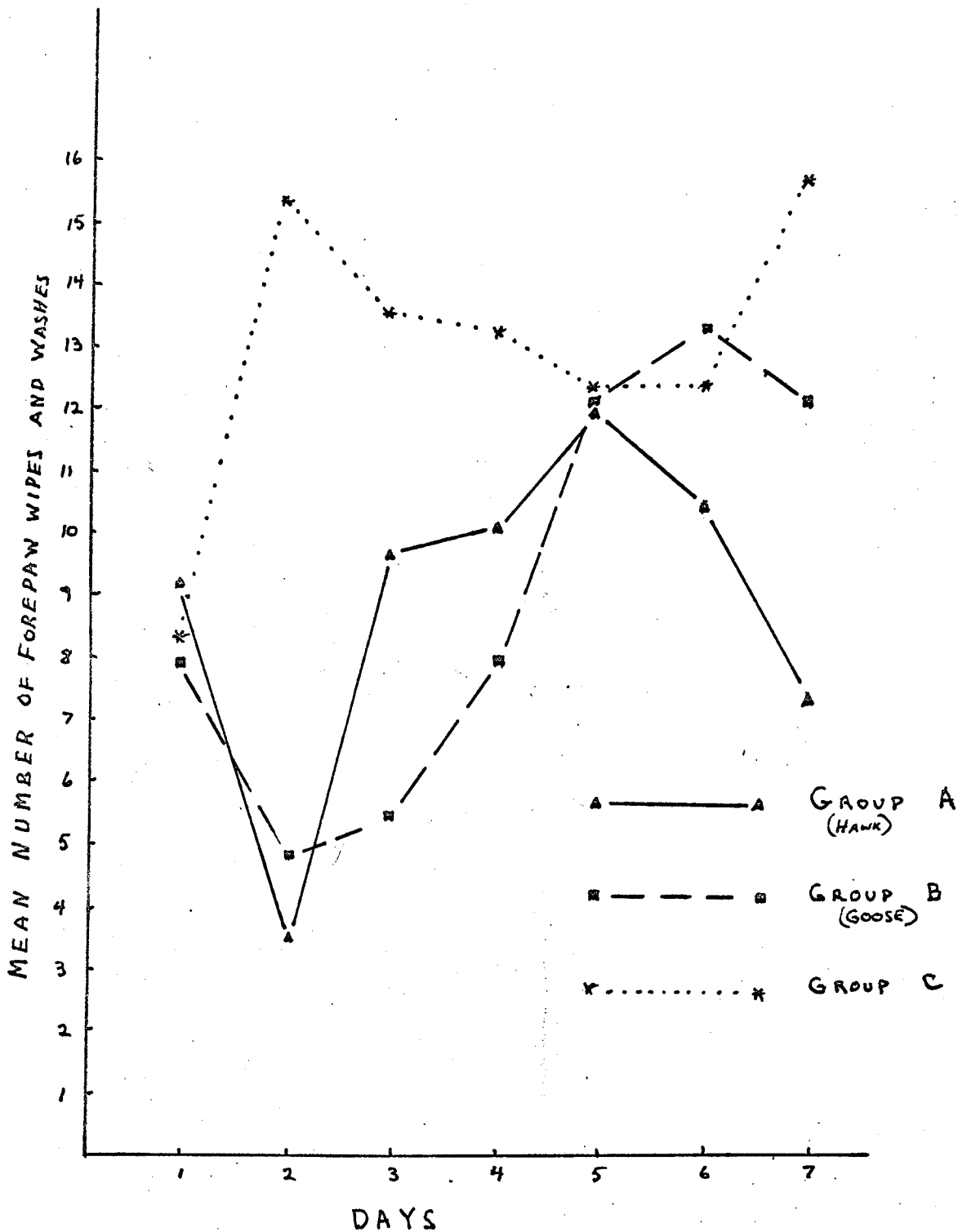TERRITORIAL MARKING OVER DAYS

FIGURE 8

DIGGING SCORE OVER DAYS

FIGURE 9

FOREPAW WIPES AND WASHES PER GERBIL

CHAPTER IV

DISCUSSION

The data undeniably support the hypothesis of an anti-predator response, and/or its ancillary startle response, to a visual stimulus that is novel when presented in a given stimulus situation. As the topography of the startle response closely parallels the anti-predator response, as defined, so it must be considered to be a variant of it, the major distinction being that the latter is consummated with leaving the open field. Their affinity is characterized with the following entry noted from a session on the first day of stimulus presentation, day two.

> Subject 13, male, group A: Startle responses to the first six presentations interlaced with foot-stomping and freezing. On the last two presentations the subject 'discovered' the enclosure and withdrew to it immediately with each presentation.

The sequence of occurrence in this case was comparatively rare and most changes in response went from anti-predator to startle responses. From the variability between subjects and the consistancy within subjects, after the initial mode of response was taken, some evidence exists for the position that the first response influences the course of the succeeding responses. The fact that four of the eighteen experimental subjects did not exhibit the anti-predator response in forty-eight stimulus presentations is not attributed to the lack of integrity of the reaction, as startle responses occurred in its place. The variability of the anti-predator response is more reasonably credited with the relative novelty of the field and that stimulus presentations occurred while the subject was anywhere in seventy-five percent of the field.

The fact that no overall significant differences occurred between groups A and B for the anti-predator response does not abridge the fact that differences of a qualitative nature were found. Both the frequency of the anti-predator and startle responses originate at near the same point on the first day of presentation (see Figure 4). Hawk-like Stimulus Group (A) then dropped to a point at which it was significantly different from the goose-like stimulus group and never did it decline to the rate of Goose-like Stimulus Group (B). The goose-like stimulus then retained its potential to elicit responses for a longer period than did the hawk-like stimulus.

The only significant effect of counter-balancing on day seven was an increase in startle responses for Hawk-like Stimulus Group (A). The anti-predator response also did increase to a greater extent in group A then group B on day seven, when the goose-like stimulus was presented to the previously hawk-like stimulus exposed group. As a similar increase was not observed in the group presented with the hawk-like stimulus for the first time on day seven there would seem to be some argument for recognizing the goose-like stimulus as being more threatening. This position is reinforced by the relatively slow response decrement that was also found for the Goose-like stimulus Group (B).

Related to the occurrence of the startle and anti-predator responses the data from the other five dependent measures (ambulation, time in the enclosure, the frequency of marking, grooming and digging) all bore consistant trends.

Initial high startle and anti-predator responses occurred with increased time spent out of the field and suppression of ongoing behaviors as ambulation, territorial marking, grooming and digging. As habituation took place to the stimulus presentations over days, as shown in Figure 4, the corresponding increase in other behaviors of biological import can be seen in Figures 5, 7, 8 and 9. This then constitutes actual experimental evidence supporting the widely held and generally non-experimentally supported assumption that habituation permits the waning of responding to biologically irrelevant stimuli in favor of biologically relevant behaviors (Lorenz, 1965; Marler & Hamilton, 1966).

The variables used in this study were parameters of perceptual experience which were demonstrated to elicit avoidance and then approach to a strange object. The waning of responses to new stimuli are not incompatible with views on exploration expressed, for example, by Glanzer (1958) and Berlyne (1960). Glanzer explains waning of responsiveness with the concept of stimulus satiation, a quantity of which builds up when an organism observes a stimulus. Using a concept which is functionally the inverse of stimulus satiation, Berlyne hypothesizes that for an individual organism at a particular time there is an "optimal influx of arousal potential" that may oscillate upward and downward. Response waning through habituation is explained by Berlyne as the loss of arousal potential by the corresponding increase in recognition of the stimulus. The similarity of these concepts with the various forms of habituation as

discussed by Thorpe (1965) is evident.

The higher arousal potential of the goose-like stimulus, which is also evidenced by the increased time in enclosure and decreased grooming from goose-like stimulus counter-balancing in Hawk-like Stimulus Group (A), might well be related to the fact that the hawk-like stimulus entered the field with its broad wings almost immediately apparent. By entering the field from between two and four feet away from the gerbil in this manner the hawk-like stimulus presented initially a larger and more complex stimulus than the goose-like stimulus's long-neck. As the stimuli were usually instantaneously reacted to when they entered the field, group A would have had a larger, more complex stimulus to discriminate than Goose-like Stimulus Group (B). The larger, more complex nature of the part of the hawk-like stimulus that was reacted to would also explain the stimulus-specific response decrement that was found in group A and not group B, as before counter-balancing in group A recognition of the hawk-like stimulus would have taken place because of its initial comparative size and complexity. Using the argument of Berlyne (1960) for the necessity of recognition of the stimulus to take place before the decline of the 'arousal potential', the goose-like stimulus group initially would have less to recognize and therefore take longer to habituate. When counter-balanced on day seven with hawk-like stimulus its novelty is not discriminated because comparatively little recognition took place previously to the goose-like stimulus. Rather than drawing on arguments

for the goose-like stimulus resembling some natural predator, as for example a snake, this more parsimonious explanation of the partial group differences is also more compatible with the evidence.

Gray (1966), in a history of the anti-predator problem, deduced four possible variables for the anti-predator response. The first was the possibility of an alarm call by the prey influencing the anti-predator reaction. No audible vocalizations occurred in response to presentations of the stimuli in this study, although an accoustical response was sometimes observed. Foot-stomping did occur infrequently and may have a communicatory function, as Kirmiz (1962) suggests in the jerboa; in this case as an alarm signal. In the colony room when foot-stomping occurred in one visually isolated cage frequently ongoing behaviors as digging would cease in adjacent cages as individuals assumed an upright position. Further stimulation would some-times elicit foot-stomping in these adjacent cages after the initial social facilitation. The dry soils noted by Tanimoto (1943) and subterrianian life of the gerbil along with its higher nocturnal activity would suggest the pos-sibility of foot-stomping functioning as a conspecific arousal mechanism for predation. Such unanswered questions reinforce Schleidt's (1961a) advice for conducting initial field study before the experimental examination of anti-predator responses.

The second variable suggested by Gray (1966) is the possible effect of social hierarchy on the evocation of the anti-predator response. As no

behavioral studies have been made of social hierarchies in gerbils and the
present study ran subjects individually, it is not possible at this time to make
any definite statements about the significance of this parameter. The finding
that males spent more time in the field in the experimental groups suggests the
possibility that males would be more likely to emit foot-stomping. The comple-
mentary fact that females spent more time in the enclosure, as compared with
albino and hooded rats where no sex differences were found in startle responses
to pistol shots (Moyer, 1963), suggests the possibility that females are more
biologically valuable than males, for example, during pregnancy.

Age is the third variable suggested by Gray (1966) in his analysis of the
anti-predator reaction. Although age was not under study in this present
analysis of the anti-predator reaction in the gerbil, observations suggest that
it occurs at least by the time of weaning, that is about twenty-six days of age.
The age of onset of the response and, in particular, the ontogenetic aspects
of the response, deserves systematic investigation.

Gray (1966) gives potential cover as the fourth possible variable in the
evocation of the anti-predator response. As stimulus presentation did evoke
definite startle reactions without the use of the enclosure for dover, potential
cover can not be considered to have been a critical variable in the compara-
tively new setting used for this study for the elicitation of an escape reaction.

The response decrement of the findings in this study must be classed as
'long-term' habituation (Thorpe, 1965). This is to be contrasted with

'short-term' habituation as found in some aspects of approach and withdrawal responses to a shadow stimulus in <u>Lebistes reticulatus</u> by Russell (1967). Among other predator reactions, long-term response decrement has been found by Schleidt (1961b) for alarm calls given by young turkeys to various moving silhouettes. Earlier Hinde (1954) found 'long-term' habituation of mobbing responses given by chaffinches to repeated presentations of live or model owls over days. Similar decrements of freezing responses given by Bobwhite quail have been found over days to two different species of hawk using direct observation and suppression of V.I. operant behavior as dependent measures (Martin & Melvin, 1964; Melvin & Cloar, 1969). Emlen (1969) reports a similar decrement in mobbing of wild birds to a 'squeak lure'.

Thorpe (1965) included the necessity of no reinforcement following stimulation in the definition of habituation. Lorenz (1965) objected to the inclusion of lack of reinforcement in the definition of habituation on the gounds that it was non-functional. Others, as Emlen (1969), have made use of this stipulation to explain response waning, arguing that habituation occurred because of the lack of reinforcement that would normally be achieved in some aspect of direct exposure to the predator. Melvin & Cloar (1969) used direct exposure of Bobwhite quail to a Swainson's hawk and habituation still occurred leaving some actual aspect of the attack before capture to provide reinforcement if this stipulation is to hold up in practice. It is perhaps useful to recall Schleidt's (1961a), and Later Lorenz's (1965), admonishment that the

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high frequency and fixed stimulus setting of exposure to predator stimuli, with other possibilities as the lack of social hierarchy noted by Gray (1966), render most all of the experimentation done on the problem artificial when compared with the natural setting. This includes the present study.

The process of habituation to stimuli has been noted as having severe drawbacks if it were to generalize to predators as well (Hinde, 1954; Lorenz, 1965). In the case of the startle and anti-predator responses in gerbils habituation can not be said to have occurred to the stimulus entering the field. Response habituation, not stimulus habituation in toto, occurred in that while startle and anti-predator response decrement was found after successive presentations the stimulus was still effective in at least eliciting a head orientation. Melzack (1961) found a similar result in mallard ducks when after two thousand presentations of stimuli head orientations were still found. Analogously Martin & Melvin (1964) found fear responses being replaced by orienting responses after Bobwhite quail had been exposed to a hawk a number of times. In this manner habituation of species specific responses to potential predators substituted by head orientation permits the possibility of the discrimination of new cues from the potential predator that might signal attack from an otherwise irrelevant stimulus. A somewhat similar situation occurs when territorial birds permit unchallenged, yet observed, "flyovers" of their territory by neighboring birds when cues precipitating a conspecific territorial encounter are presumably absent.

Experiments concerning predator stimuli have shown that generalization,

or transfer, of habituation from one stimulus to another to be a common

phenomenon. The waning of the responsiveness to one stimulus often carries

over, in part, to the response evoking properties of another stimulus. This

was certainly the case for the startle and anti-predator responses of the

gerbil. Stimulus-specific response decrement only occurred to some extent

in group A, when stimuli were counter-balanced on the seventh day and the

level of response at this time did not approximate the high frequency found

initially. Similar results were reported by Hinde (1954) for mobbing

behavior of chaffinches, which consists of approach and 'chink' calls. In

one series of experiments Hinde found that birds initially exposed to a

stuffed owl showed a considerably reduced level of responding when exposed

to a live grass snake than those not previously exposed to the owl. Martin

& Melvin (1964) found that Bobwhite quail first exposed to a model of a hawk

showed less responsiveness to a live Red-tailed hawk than those birds not

first exposed, this in spite of the fact that the live hawk elicited a consider-

ably greater response than the model hawk when both were presented for the

first time. Similar results were reported by Melvin & Cloar (1969) using

Bobwhite quail exposed to pigeons perched followed by a Swainson's hawk

perched having interruption of a V.I. schedule of operant responding by

freezing as a dependent measure. Thus in varying degrees response habi-

tuation is found with stimulus habituation.

One factor not controlled for in most experiments relating to habituation

is the effect of the "predator stimulus in a particular place" as compared with
just the predator stimulus. Hinde (1954), in the most extensive study of
habituation processes in birds, found that the stimulus setting does effect
habituation rate. By changing the surroundings of subject and stimulus,
habituation was retarded and it is reasonable to think that the constant stimulus
setting facilitated response decrement to stimulus presentations in the gerbil.
The involvement of the method of presentation and stimulus setting would help
account for the small amount of stimulus specificity in the response waning, as
shown in counter-balancing.

Handling of preweaned rats has been found to increase activity and decrease
defecation. These findings lead DeNelsky & Denenberg (1967) to conclude that
handled rats are "less emotional." Infantile handling resulted in the rats being
more "exploratory, or curious," than non-handled controls. Should this finding
generalize to gerbils, and gerbils in a post-weaned state, the results of this
study may have been effected. Post-weaned gerbils in this study were handled
and exposed to the new environment of the holding cage, a similar procedure to
experimental handling, during the weekly cleaning of home cages, possibly
decreasing their reactivity to experimental stimuli. Since gerbils in the natural
habitat would not be handled by humans, they would consequently be more reactive
to experimental or naturally occurring stimuli than gerbils in this study. As
Schleidt (1961a) suggests generally, to be properly understood the anti-predator
response in gerbils must be studied, at least in part, under field conditions.

Schneirla (1959;1965) has developed a sophisticated theory of biphasic approach and withdrawal behavior for inter-specific application. Cast in an evolutionary perspective, Schneirla's argument is that each species has undergone natural selection for optimal approach and withdrawal gradients, and their corresponding physiological substrates, to optimal intensities of stimulation. Synoptically, Schneirla contends "low intensities of stimulation tend to evoke approach reactions, high intensities withdrawal reactions with reference to the source (1959, p. 513)." The initial startle and anti-predator responses of the gerbil, due to their topography, can be viewed as withdrawal responses and, after their waning, movements toward the stimulus source and "air-testing" as approach responses. Schneirla's (1959; 1965) consumptive use of quantitative effects in explanation of behavioral processes did not, however, make use of the process of habituation in his analysis of the anti-predator reaction and criticism of Tinbergen (1948). Instead Schneirla (1965, p. 16) attempted to explain the hawk-like stimulus reaction as being a result of a "sudden massive increase in retinal stimulation," as opposed to the gradual increase in the case of the goose-like stimulus. This led Schneirla (1959) to hypothesize that a base forward triangle would elicit hawk-like responses and a apex forward triangle, goose-like responses. Green, Green & Carr (1966) examined this hypothesis experimentally with mallard ducks and found higher responses to the hawk-shaped stimulus and lower responses to the goose-shaped stimulus and triangles sailing in both directions. Thus Schneirla's 'intensity' hypothesis was not supported.

CHAPTER V

SUMMARY AND CONCLUSIONS

Fourteen female and thirteen male Mongolian gerbils, *Meriones unguiculatus*, were randomly assigned in equal numbers to three groups at one-hundred and eighty days of age. Groups A, B, and C, with nine gerbils per group, were each exposed to a gridded, open field with a small enclosure for twenty minutes per day, for seven consecutive days. From days two to six groups A and B received eight presentations per day of a hawk-like and goose-like stimulus, respectively. The dependent measures recorded observationally included the frequency of startle and anti-predator responses, ambulation, time spent in the enclosure, territorial marking, grooming and digging.

It was hypothesized that (a) an anti-predator response occurs in the gerbil to a visual stimulus, (b) differences in responsiveness occur for the gerbil to short and long-necked stimuli and (c) stimulus-specific response decrement occurs for the anti-predator response in the gerbil.

The results substantiate the occurrence of the anti-predator response, and its ancillary startle response, to a visual stimulus in a given situation. No overall differences were found between groups A and B, although the goose-like stimulus had a comparatively lower rate of response waning. Only partial stimulus-specific response decrement was found, which occurred in group A, as indexed by the increase in startle responses to the counter-balancing stimulus. Basal observations revealed initial high rates of startle and anti-predator responses occurred with increased time in the enclosure and suppression of ongoing

behaviors as ambulation, territorial marking, grooming and digging. As responses to the stimulus presentations waned time in the enclosure decreased and ongoing behaviors increased in occurrence.

The results were interpreted as supporting the findings of Hinde (1954), Melzack (1961), Schleidt (1961a), and Martin and Melvin (1964) that 'long-term' habituation occurs to predatory-like stimuli with successive presentations. The findings substantiate the anti-predator reaction in the gerbil as a natural response mode open to experimental analysis and shows how a paradigm originally framed for avian species can usefully be exploited for species-specific mammalian behavioral analyses. Furthermore, the findings related to ongoing behaviors constitutes actual experimental evidence supporting the widely held and generally non-experimentally supported assumption that habituation permits the waning of responding to biologically irrelevant stimuli in favor of biologically relevant behaviors.

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APPENDIX