Portland State University

PDXScholar

5-1973

Agonistic Behavior and Dominance in Townsend's Chipmunks (*Eutamias townsendii*)

Paul Evan Sherman
Portland State University

Follow this and additional works at: https://pdxscholar.library.pdx.edu/open_access_etds

Part of the [Biology Commons](#)

Let us know how access to this document benefits you.

AN ABSTRACT OF THE THESIS OF Paul Evan Sherman for the

Master of Science in Biology presented May 18, 1973 .

Title: Agonistic Behavior and Dominance in Townsend's

        Chipmunks (<u>Eutamias townsendii</u>).

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:

_____

        Richard B. Forbes, Chairman

_____

        John H. Wirtz

_____

        Robert O. Tinnin

        Agonistic behavior and dominance are described for

captive Townsend's chipmunks (Eutamias townsendii). A

total of 10,739 encounters was recorded; 6441 (59.9%) were

agonistic. Chases (58.5%) and displacements (30.8%) were

the predominant agonistic behaviors; threats (6.8%) and

fights (4.1%) were relatively rare. .

        Stable, non-triangular hierarchies were rapidly

established in 11 of the 12 groups of chipmunks observed;

the presence of individuals of equal rank in some groups

precluded strict linearity. Dominance positions did not change within a group, but reversals in rank and changes from equal to dominant-subordinate relationships occurred when the membership of groups was changed. One hierarchy existed for both sexes; neither sex was consistently dominant. Experience and individual differences in activity and aggressiveness were more important determinants of an animal's position in the hierarchy than were sex or size. No correlation was found between rank and encounter frequency, nor was closeness of rank strongly correlated with high numbers of agonistic encounters between any two chipmunks. The frequencies of recognitory and sexual behavior were inversely related to the frequency of agonistic behavior between pairs of animals.

Ritualized threats and appeasement behaviors did not replace overt aggression in established hierarchies. Members of hierarchies showed neither a reduction in numbers of agonistic encounters, nor temporal changes in frequency of the different types of agonistic behavior. Agonistic encounters increased in frequency from August to December, but seasonal variations were much smaller than variations among the groups. Although dominance reduced neither the frequency of agonistic behavior nor the time and energy spent in chasing, it may be advantageous in curtailing harmful confrontations and enhancing the establishment of tolerance among some individuals.

AGONISTIC BEHAVIOR AND DOMINANCE IN TOWNSEND'S

CHIPMUNKS (<u>EUTAMIAS TOWNSENDII</u>)

by

PAUL EVAN SHERMAN

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

Portland State University
1973

TO THE OFFICE OF GRADUATE STUDIES AND RESEARCH:

The members of the Committee approve the thesis
of Paul Evan Sherman presented May 18,1973.

Richard B. Forbes, Chairman

John H. Wirtz

Robert O. Tinnin

APPROVED:

Earl Fisher Jr., Head, Department of Biology

David T. Clark, Dean of Graduate Studies and Research

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE

INTRODUCTION

Intraspecific fighting and aggressive behavior are
common phenomina in many animals, yet have potentially
deleterious effects. Injury or death, energy and time
expenditure, and increased vulnerability to predation are
all manifestations of fighting, thus making its restric-
tion of considerable importance (Tinbergen 1965). Terri-
toriality restricts fighting by dispersing members of a
species more widely, and conferring an aggressive advan-
tage to a resident over an intruder. Fighting is also
reduced by the establishment of a dominance hierarchy.
Through recognition and memory, subordinate animals learn
to avoid or relinquish position to dominant individuals,
and to dominate those of lower rank. In many species,
an initial period of overt conflict is supplanted by a
preponderance of ritualized threat behaviors in addition
to an overall reduction in agonistic behavior. The
function and selective advantage of this occurrence is
the maintenance of order by rank without suffering the
effects associated with active combat.

Social dominance and agonistic behavior in Sciuridae
have been widely studied (Anthony, Bronson, Farentinos,
Gordon, King, Sheppard and Yoshida, and Yeaton). Despite

the suitability of chipmunks for behavioral studies, investigations of these animals have been relatively meager. The eastern chipmunk (_Tamias_) has been the subject of many more papers than has its more widely distributed and variable western counterpart (_Eutamias_). Descriptive field studies on _Tamias_ have been done by Fraleigh (1929), Burt (1940), Yerger (1953), and Dunford (1970) among others. Condrin (1936) and Wolfe (1966) have studied captive _Tamias striatus_.

Descriptive field work on agonistic behavior has been done for _Eutamias_ in general (Gordon 1936, 1943) and for _E. amoenus_ (Broadbooks 1958, 1970). Interspecific agonistic behavior has been investigated by Brown (1970), Heller (1970), and Sheppard (1971). Brand (1970) devoted a portion of his study on chipmunks in California to agonistic behavior and dominance in _E. townsendii_. Quantitative information on agonistic encounters and dominance relationships was included in studies by Condrin (1936) and Wolfe (1966) on _Tamias_, and by Brand (1970) on _Eutamias_. Brown (1971), Brand (1970), and others indicated that agonistic behavior in the field was qualitatively similar to that of captive animals.

The present study categorizes and describes agonistic behaviors and dominance hierarchies in captive _Eutamias townsendii townsendii_. A qualitative and quantitative analysis of the observed behavior patterns

related to the formation and development of dominance
relationships is presented.

METHODS OF STUDY

Twelve groups of four chipmunks (E. townsendii)
each were used in the study, which began 1 August 1972
and ended 1 January 1973. A total of 230 hours of obser-
vation was logged. The chipmunks were housed in two
cages measuring 8 x 8 x 6½ feet high, located outside,
on the roof of Science Building I at Portland State
University, Portland, Oregon. The cages were constructed
of ½ x 1 inch mesh wire supported by a wooden frame. A
slanted, green fiberglass roof afforded partial cover
from rain and sun. The floor was covered with about
three inches of fine wood chips, leaves, and sticks. Each
cage had ten wooden nest boxes along one wall, with
cotton available for nest material. Some of the nest
boxes had no tops and were used by the chipmunks only for
escape; the others contained a single entrance two inches
in diameter. Several logs with branches were present,
and a block of wood was attached to the wall of each cage.

Water was available ad libitum in a single large
trough in each cage. Food was placed in a small tin or
scattered around the ground. Food was normally in abun-
dance, but several times was withheld for a short period
to study the effect of low food supply on agonistic

behavior. Oatmeal made up the staple food during the study, but other items including raisins, nuts, watermelon seeds, and peanut butter were occasionally available. Most items that could be carried by the chipmunks were taken into the nest boxes or buried.

The chipmunks were caught in the southwest Portland hills by means of Sherman live traps baited with peanut butter. The area is one of steep slopes dominated by mature Douglas-fir trees (Pseudotsuga menziesii). The chipmunks were weighed, sexed, and toe-clipped for perminent identification. A patch of fur was dyed on each individual to allow for easy recognition of the chipmunks in the cages. I remarked the animals as necessary.

Observations were made through the window of a room situated three feet from the cages. Both cages were observed daily, but never simultaneously. Periods of observation varied from 15 to 60 minutes each, and were spread throughout the day between dawn and dusk. Yerger (1953) and Brand (1970) observed that chipmunks have two peak periods of daily activity in the wild; in this study their diurnal activity cycle was unpredictable. Activity became intense after the food tin was filled regardless of conditions or time of day, even if more oatmeal was added to an already abundant supply.

The periods of study for the cage groups varied from

7 to 37 days. Since observation periods for each group were not uniform, agonistic confrontations are presented in this paper as encounters per hour for the purpose of comparison.

After the first month of observation, one chipmunk from each cage was moved to the other cage, thus creating two new groups of different membership. Twelve distinct groups were formed in this manner using the eight original chipmunks plus another captured late in October to replace one of the original subjects. By employing the same nine animals in 12 different combinations, the relationships between any two individuals was observed several times, but in the presence of different chipmunks. In addition, each chipmunk was observed in five to seven distinct social situations. This enabled comparison not only of agonistic behaviors and dominance hierarchies among cage groups, but provided data on the stability of pair relationships. Individual variations and some seasonal differences in frequency of agonistic encounters under various social conditions were also determined. One group of four animals studied in August was placed together again in December to compare behaviors.

In addition to recording all agonistic encounters (N=6441), all non-agonistic encounters (N=4298) were recorded to investigate relationships between dominance and various other social behaviors. The type and

participants of all encounters were recorded chronolog-
ically in the study, with observations separated by cage
group. Dominance was determined by analyzing encounters
between each pair of individuals, with the animal who
chased, threatened, or won a fight declared the winner.
Chi-square tests were used to determine if the margin of
victories over defeats was statistically significant
($p < .01$). If it was not, the two chipmunks were consid-
ered equals. Thus, dominance hierarchies were ascertained
in each group, and the number of subordinate victories and
switches in dominance investigated.

Variations in agonistic behaviors over a period of
time were investigated. First, I attempted to determine
whether changes in frequency, and/or frequency of types,
of agonistic encounters occurred during the 7 to 37 day
periods each cage group was together. Encounters during
successive three day intervals were presented graphically.
I also attempted to determine whether there were seasonal
variations in agonistic behaviors between August and
December. The total number and the number of each type
of encounter during successive 15 day intervals were
graphed, to detect any significant pattern in frequency
of encounters from summer to fall and winter.

RESULTS

I PATTERNS OF AGONISTIC BEHAVIOR

I observed 10,739 encounters between captive
E. townsendii; 6441 (59.9%) were agonistic. Five types
of agonistic behavior occurred- chases, fights, threats,
displacements, and escapes.

Chases

Chasing was the most frequent agonistic behavior,
comprising 58.5% of the total. Length of chases varied
from a few feet or less to repeated swerving laps around
the floor and wall of the cages. Speed of chase also
varied. It was common for a dominant to chase a rival
a dozen or more times in succession. One animal chased
a rival 782 times in their period together without
apparent waning of the tendency. The reaction of the
subordinates, even to repetitive aggression, was a seem-
ing absence of increased avoidance or isolation. Subor-
dinates continually approached and were chased away by
aggressive dominants. On other occassions, the subordinate
did not withdraw from an approaching high-ranking animal.
The latter then either attacked and chased the defiant
chipmunk, ignored it, or approached and threatened or even

nudged the subordinate into flight.

Chipmunks in this study most often engaged in chases without preliminaries (90%), but chases subsequent to fights or threats (10%) also occurred. Only 13 of 3769 chases were initiated by subordinate individuals. Chase behavior normally began when a dominant animal, while exploring the cage, came upon a subordinate and immediately gave chase. Dominants did not appear to look for subordinates to chase. Chase was also elicited by the approach to a dominant of a subordinate. The latter usually began running before the dominant began to chase. Most chases ended with the dominant giving up and resuming other activities. Subordinate chases ended similarly, but were shorter. During these encounters, both participants ran with their tails straight out or slightly above parallel to the ground.

Fights

Fighting as used here included any physical contact of an apparently aggressive or hostile nature. Fighting in my E. townsendii was infrequent (4.1% of observed agonistic encounters) and of a mild nature. One hundred ten of the 261 fights involved two individuals grasping each other and tumbling about, while biting at and clawing each other. These bouts occurred when a dominant overtook a pursued subordinate, and lasted several

seconds. Frequently the subordinate broke away, but sometimes the dominant did so immediately after catching the subordinate. This was particularly evident with WH, the alpha chipmunk of my study population, who would race to a nest box almost immediately after contact. Chase-fight-chase sequences were also observed commonly (20% of all fights).

A less frequent precursor to fighting was observed almost exclusively within the first few days I placed a group of chipmunks together, presumably when dominance hierarchies were being established. Two chipmunks would approach each other head-on until separated by a distance of approximately 10 centimeters. They would then chase each other in small circles, concluding with a fight. The preliminaries took only a few seconds, and although the bouts appeared more intense than usual, they still lasted only 3-4 seconds. The fight concluded with one chipmunk (victor) pursuing the other (loser).

Boxing (sparring with forefeet while standing erect on hind legs) occurred 67 times. This behavior occurred only after one chipmunk attempted to mount another. The normal procedure for the mounted individual was to move straight out of the grasp of the other, or occasionally to remain in a crouched position until the mounter gave up. In 67 of the 779 observed mountings (9.0%), the animal on the bottom would turn, and, while both chipmunks

were erect, strike with the forefeet its opponent's head and upper body. The other chipmunk would immediately retaliate in the same manner, using quick and repeated blows. In 60 of the 67 cases (88.0%) the chipmunk initiating the boxing was dominant. No attempt to bite the opponent was evident, and the confrontations ended without further agonistic behavior.

Attacks resulted when a low ranked individual did not move when approached by an aggressive dominant (65 cases), or when a dominant caught another chipmunk by surprise (19 cases). These encounters involved the dominant striking with its paws and lunging at the subordinate, and/or biting at the subordinate, who would then withdraw, sometimes with the aggressor in pursuit. On a few occasions (5), when dominance was not yet established, an attack-withdraw-attack sequence was observed.

Threats

Four hundred forty one threats (6.8%) were observed. Although chipmunk threat behavior is not highly stereotyped (Brand 1970 and Wolfe 1966), four forms of threat were recorded. Threats occurred in a variety of situations and involved many postures. A detailed analysis of postures was not attempted. In the freeze threat, the threatening animal stares at its rival although the two animals' bodies may be perpendicular to each other. Gen-

erally, the threatening chipmunk's head is up, body
straight or slightly arched, and tail straight out or up.
Occasions of tail waving in a slow, up and down or fast,
jerky motion were observed, but were not a necessary
component of the threat posture. Erection of the body
hair was not noticeable, but tail hairs were slightly
erected.

In the first few encounters, the threatened chip-
munk would assume a position similar to that of the
threatening chipmunk, and the two would exchange stares
for up to 15 or 20 seconds. The distance between animals
varied. On a number of occasions, the threatened or
threatening individual would groom itself or turn in a
different direction. Among chipmunks familiar with each
other, a threat engendered a different reaction. A
threatened subordinate either withdrew or turned its body
and head down or perpendicular to the threatening domi-
nant. It appeared that the crouched body position or
turning away movement appeased the aggressor to some
extent, for few chases occurred after this behavior.
Another appeasement behavior was the lowering of the
head or "bowing" when a superior approached or turned to
face a subordinate chipmunk. Chases sometimes followed
threats despite appeasement behaviors.

"Threat to chase" by a dominant involved quick,
jerky movements toward a subordinate chipmunk that ended

when the latter withdrew. The movement was accompanied
by a thrusting forward of the head. On a number of
occasions a dominant would bite at an opponent, or raise
a foreleg and swipe at it even though the other chipmunk
was well out of range. These actions were termed "threat
to attack" and always caused a hasty retreat by the
subordinate. Often the feet did not move at all in the
behavior; only a forward thrust of the head and body
occurred. Also, the foreleg was sometimes merely raised
and not directed at the opponent.

A fourth type of threat, termed "turn threat",
occurred when a subordinate approached an aggressive dom-
inant from behind. The dominant, when it sensed the
subordinate's approached, would turn its head rapidly to
face to face the subordinate. This led to the subordi-
nate's rapid retreat. The threat lasted only a brief
interval, as did the chase and attack threats.

Displacements

Displacements took place when a low-ranking chip-
munk relinquished its position to an approaching dominant,
regardless of whether the latter appeared cognizant of its
rival, and before any aggressive behavior took place. I
observed 1971 (30.8% of agonistic encounters) displace-
ments during the study. Displacement most often occurred
at the food dish, the most likely spot for two caged

chipmunks to meet. The intensity of aggression between any pair was reflected by the distance from a dominant at which the subordinate withdrew; greatly harassed animals retreated earlier than more tolerant ones.

Escapes

Escape behavior in E. townsendii entails rapid running away from any feared stimulus. The pattern of escapes of captive chipmunks was curious in that a rather elaborate chase-escape route was often employed which was navigated repeatedly until the chase stopped. Since most of the animals had places outside the nest boxes where they were most often found, the same routes of escape were observed a considerable number of times. Although E. townsendii are reported to be the most arboreal of their genus (Dalquest 1948 and Tevis 1956), most routes in the cages stuck to the ground or over objects on the ground. When a pursued chipmunk broke its pattern and climbed the side of the cage, it was rarely chased further. At other times, chipmunks spent a great deal of time climbing around the sides and also walking upside down across the ceiling of the cages. Agonistic behavior was rarely observed to occur from either position, even when intolerant chipmunks met. One animal (WT) developed an escape route that featured running to a certain point, then turning suddenly and

jumping directly over its pursuer and continuing in the opposite direction. Many of the subordinate chipmunks were seen running the same patterns alone that they often ran when chased. Other chipmunks were seen running routes with great repetition which they never used during a chase, and some, including the alpha chipmunk, never ran a discernable pattern.

II DOMINANCE HIERARCHY STRUCTURE

All but one of my 12 cage groups established a stable, non-triangular hierarchy. Figures 1 and 2 indicate the results of encounters in each group. Interactions between individuals in 16 of the 72 dyads did not justify designation of individuals as dominants or subordinates ($p > .01$). A linear chase order could not be constructed for the nine chipmunks by combining the results of dominance relationships in the various four-member hierarchies. Thus, to describe the hierarchies as strictly linear would be inaccurate.

Once established, dominance positions never changed in any one cage group. Dominance positions and hierarchical patterns did change, however, when a new chipmunk was added to a group. The highest and lowest ranks tended to be stable and predictable when chipmunks were relocated; the middle positions were less well defined.

GROUP A (Aug 4-31)

winners

	RH	WH	RT	WT
RH	X	2	3	0
WH	6	X	2	2
RT	210	86	X	1
WT	48	18	82	X

GROUP A2 (Aug 8-31)

winners

	WH2	YH	WT2	O
WH2	X	2	3	0
YH	3	X	8	9
WT2	5	11	X	1
O	3	6	16	X

GROUP B (Sept 1-14)

winners

	WH	RT	WT	O
WH	X	0	1	0
RT	42	X	3	0
WT	15	76	X	0
O	156	77	238	X

GROUP B2 (Sept 1-14)

winners

	RH	YH	WH2	WT2
RH	X	0	0	0
YH	56	X	0	0
WH2	21	3	X	0
WT2	60	0	0	X

GROUP C (Sept 15- Oct 8)

winners

	WH	WH2	WT	O
WH	X	0	0	0
WH2	24	X	9	0
WT	36	7	X	0
O	293	140	324	X

GROUP C2 (Sept 15- Oct 6)

winners

	RH	YH	WT2	RT
RH	X	5	1	0
YH	65	X	2	1
WT2	44	2	X	4
RT	251	226	34	X

Figure 1. Results of agonistic encounters in six groups observed between August 1 and October 8, 1972. Wins are recorded vertically and losses horizontally.

GROUP D (Oct 9– Nov 15)

winners

	WH	WH2	YH	O
WH	X	0	0	0
WH2	48	X	5	0
YH	100	51	X	1
O	375	247	777	X

GROUP D2 (Oct 9– Nov 13)

winners

	RH	RT	WT2	WT
RH	X	1	0	0
RT	15	X	1	0
WT2	13	10	X	1
WT	30	27	27	X

GROUP E (Nov 15–22)

winners

	WH	YH	WT2	O
WH	X	0	0	0
YH	28	X	0	0
WT2	6	18	X	0
O	100	176	1	X

GROUP E2 (Nov 15–22)

winners

	RH	RT	WT	WH2
RH	X	1	0	0
RT	51	X	0	0
WT	21	8	X	0
WH2	34	5	24	X

GROUP G (Nov 27– Dec 19)

winners

	WH	RT	O	YT
WH	X	0	0	0
RT	157	X	0	0
O	112	242	X	2
YT	135	224	50	X

GROUP H (Dec 19–31)

winners

	WH	RH	WT	RT
WH	X	0	0	0
RH	21	X	3	0
WT	27	25	X	2
RT	39	116	243	X

Figure 2. Results of agonistic encounters in six groups observed between October 9 and December 31, 1972. Wins are recorded vertically and losses horizontally.

The most marked alteration occurred in the relationship between RT and WT, both in the middle of the hierarchy. In the first four periods the pair was together, RT achieved a total of 193 wins in 197 agonistic encounters, chasing WT persistently and intensely during the initial two periods, and infrequently the last two. When placed together for the fifth and final time, at the end of the study, WT reversed dominance completely, winning 243 of 245 encounters.

A shift also occurred between the two alpha chipmunks in cage A, RH (male) and WH (female). Placed together originally, the two were co-dominant, although RH was much more aggressive toward the other cage members. RH and WH lived in the same cage for a month with only eight displays of agonistic behavior between them; RH won six. The two were again placed together the last 15 days of the study; this time WH was clearly dominant. The number of confrontations was still small (21), but WH won all. On eight other occasions when a pair of chipmunks was reunited, the relationship changed from that of equals to dominant-subordinate or from dominant-subordinate to equals. In all cases of equality (16), the number of agonistic encounters was minimal, ranging from 0 to 19 and averaging 7.0. The rate of agonistic behaviors between equals was less than 8% of the average encounter frequency (28.0 per hour) during the study.

In group A2, in which no dominance hierarchy was discernable, the overall average encounter rate was 4.8 per hour, compared with 21.9 agonistic encounters per hour in group A (observed at the same time). Furthermore, the rate in A2 after the first day diminished to 1.8 per hour for the rest of the month. Five of the six dyad relationships in A2 were labeled equal rather than dominant-subordinate ($p > .01$). The other relationship, though dominant-subordinate ($p < .01$), was comprised of only 17 encounters, 16 won by the dominant.

Dominance hierarchies within each group were extremely stable. Of 6329 agonistic encounters between dominant-subordinate dyads, 42 (0.7%) subordinate victories were recorded. Subordinate wins were not confined to the first few encounters, but were dispersed throughout the periods the groups were together. Subordinate victories included 15 displacements, 13 chases, and 5 threats. No "grasp-and-tumble" fights were lost by dominants, but subordinates twice attacked higher ranked individuals, and seven times initiated, and were successful in, boxing with superiors.

Sex And Size Relative To Rank

Only one hierarchy existed for both sexes, and rank was irrespective of sex. Although size was of some importance in determination of rank, neither weight nor length were sufficient to explain the establishment of hierarchy

position. It was common for a much lighter chipmunk to dominate or achieve equality with a larger one. WH2, a female weighing 112 grams, was the heaviest chipmunk, yet did not dominate in any of the five groups in which she was observed. WT2, on the other hand, who weighed 78 grams, was equal with YH (97gm), O (83gm), and WH2, and dominated RT (94gm) and WT (95gm).

Territoriality

No territorial behavior was evident among my E. townsendii. The nest boxes were not even defended. On a number of occasions, three chipmunks were found together in a single nest box. As some of these observations were made in August at temperatures of 24° C., aggregation for warmth is a tenuous explanation for the observed lack of territoriality. At the food tin, chipmunks that were normally tolerated by the dominants were allowed to feed alongside them. In one cage, where tolerance between all four chipmunks was realized, the animals were seen climbing all over each other trying to get at the oatmeal in a small tin. Several times food was withheld for a short time; this brought varying results. In the groups where all were tolerant of each other, and in other instances where two or more animals were equals, agonistic behavior was absent despite apparent hunger. At other times, a dominant chipmunk chased subordinates more intensely than usual, and even chased chipmunks

normally tolerated. The chases usually did little to
deter a hungry subordinate from approaching the food
repeatedly after it was replaced, only to be chased away
each time. Low-ranking animals approached the food dish
in a cautious manner, creeping up with their bodies low,
even if the dominant was not near. Since an abundant
local supply of food is probably the principle occasion
for chipmunks to encounter each other in nature, the
apparent wariness around food is likely due to past
experience. Most feeding is done away from the food tin.
An animal would fill its cheek pouches with food, depart
to cache or eat it, then return and repeat the procedure.

Residence

Among many species of animals, the resident of a
cage has an advantage in conflicts with a new arrival,
presumably because the introduced animal is comparable to
an intruder in an already established territory (Tinbergen
1965). I did not observe this relationship among my
chipmunks. In the first change of combinations, RH, a
co-dominant with WH in Group A, was placed in the other
cage with three animals that had been housed there for
the previous month. Shortly, and with a minimum of resis-
tance, RH assumed the dominant role in his new cage. O,
conversely, became the lowest subordinate in cage I. In
the next change, newly introduced WH2, a dominant, lost a

brief but intense struggle with WH for dominance, and assumed equality with and dominance over the two other cage members. In general, determination of rank following regrouping was not influenced by previous rank.

One effect of the introduction of a new arrival into a cage of three residents was an increase in level of agonistic encounters among the residents. Among chipmunks between whom conflict had ceased or greatly subsided, sometimes for weeks previously, the actively dominant-subordinate roles resumed. Subordinates who had freely approached dominants or equals resumed cautious and hesitant manners, and approached the dominants or equals less frequently. A chipmunk with little fear of another approached with a steady, but jerky movement with the body in a normal walking position. The more fearful animals approached using a slower, more creeping movement with the body stretched out and low to the ground. Ample opportunity was available to observe the latter since even the most intensely chased subordinate occasionally approached a dominant. Less intensely chased subordinates approached frequently, usually with nose-to-anal or nose-to-nose postures, as if to seek tolerance of the dominant.

No mortalities due to fighting occurred in the five months of the study. Two animals died near the

end of the study from unknown causes. No wounds were
visible on any chipmunk throughout the study but tail
hairs of some individuals were nipped off during chases.
The fur of subordinates was noticeably rougher than
that of dominant animals, particularly on chipmunks
chased frequently. No patches of fur were pulled out
however.

Encounters Versus Rank

The relationship between number of agonistic
encounters and social rank was investigated by comparing
the total number of wins and losses for each animal to
the others in the group. In 7 of the 12 cage groups,
the lowest subordinate was involved in the most encoun-
ters and never was least involved. The alpha chipmunk,
on the other hand, was involved in the most encounters
in only two cage groups and was least involved in
three. The dominant animal had the most total vic-
tories in half of the cage groups.

The chipmunk hierarchies I studied did not conform
to the observations of other workers that closest
rivals fight most frequently and intensely (Anthony
1955; Bronson 1964; Wolfe 1966). RH and WH, alpha
chipmunks in group A, fought with RT and WT, the third
and fourth-ranked individuals, far more than with
each other. In group B, the dominant (WH) chased

fourth-ranked O approximately three times as often as
the two intermediate rivals combined. In all but two
cage groups, the dominant chased the lowest subor-
dinate with equal or greater frequency than the others.
Second-ranked individuals also chased the lowest subor-
dinate equally or more frequently than the third-ranked
animal. Dominants chased second and third ranked
individuals approximately equally. Such a chase struc-
ture reveals the reason for the high number of agonistic
encounters participated in by the lowest subordinate.
My observations indicate that the number of chases
between individuals is a reasonably good indication
of the intensity of aggression.

III HIERARCHY DEVELOPMENT

Establishment And Stereotypy

As indicated previously, the establishment of a
hierarchy among captive E. townsendii is swift, stable,
and permanent within any group. The adaptive advantage
of the hierarchy with regard to reducing fighting and
chasing, however, is minimal or at least unpredictable.
The combination of ritualization and appeasement,
typical of many species and resulting in a predominance of
threat behaviors to maintain dominance, is not seen in
E. townsendii. Serious chases and fights continued
through the duration of each cage period between some

pairs of chipmunks with no deterioration of intensity
in later stages of interaction.

Establishment of a clear dominance order took
varying lengths of time and numbers of encounters, but
never more than six or seven confrontations between any
two individuals. A common sequence of events was one or
more nose-to-anus meetings, followed by two or three
attacks or fights. Thereafter, chases and displacements
became the principle agonistic behaviors with a dominant
and subordinate role clearly defined. The rapidity of this
formation accounts in part for the extremely low number
of subordinate victories recorded in the study. No
chipmunk was observed to turn and defend itself after a
chase began. In a number of cases, a relationship was
established without conflict. That is, a chipmunk
placed in a cage with three others would chase or be
chased with no preliminary fighting, threatening, or
recognitory behaviors.

In-group Agonistic Behavior Through Time

A graphic analysis of the number of agonistic behav-
iors through time in each cage group produced mixed
results. The classical decrease of encounters through
time was seen in several cages, but was generally absent
or indistinct. Figures 3 and 4 illustrate the pattern
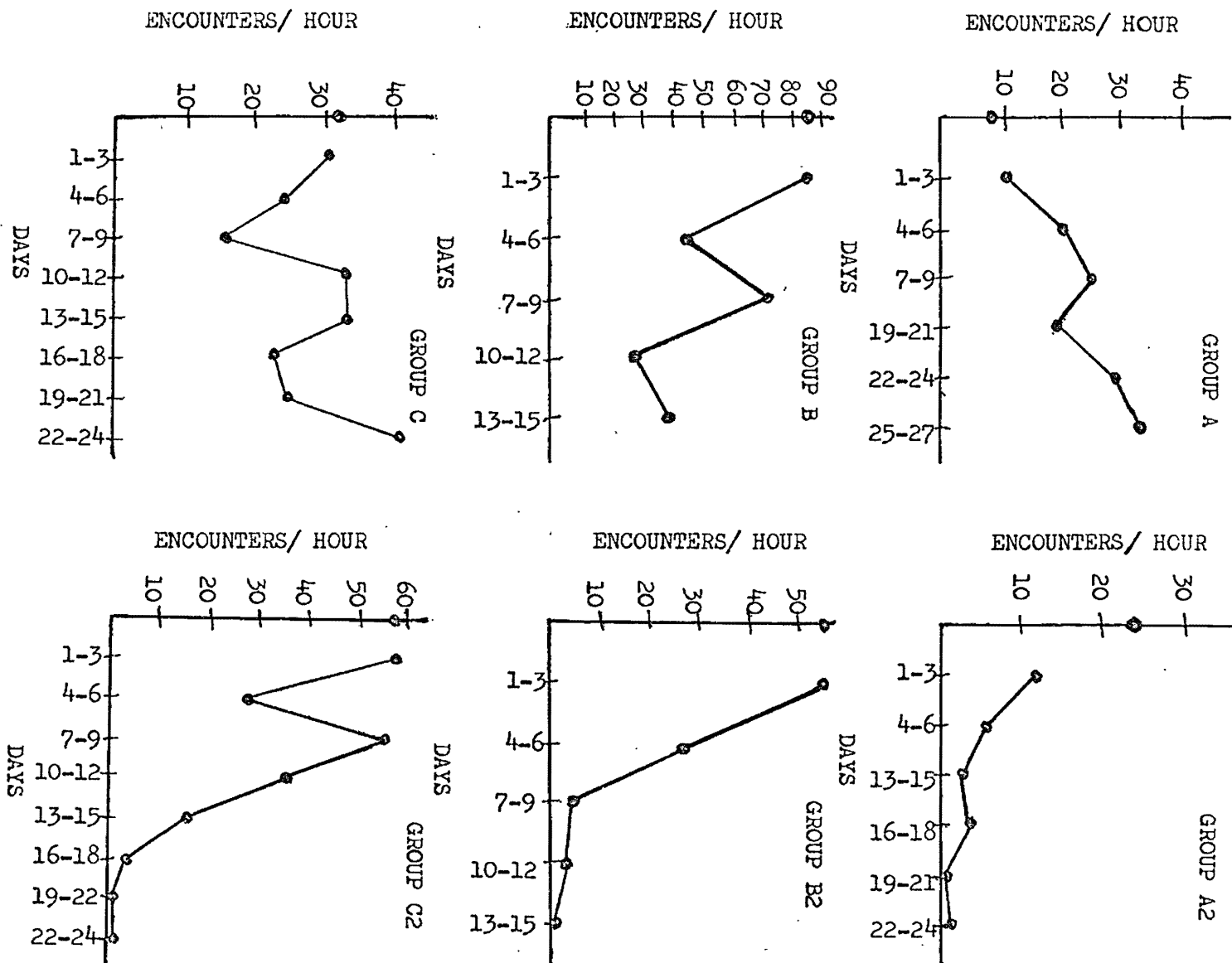in nine cages where observations were lengthy and broad

Figure 3. Frequency of agonistic encounters through time in six cage groups observed between August 4 and October 6, 1972.
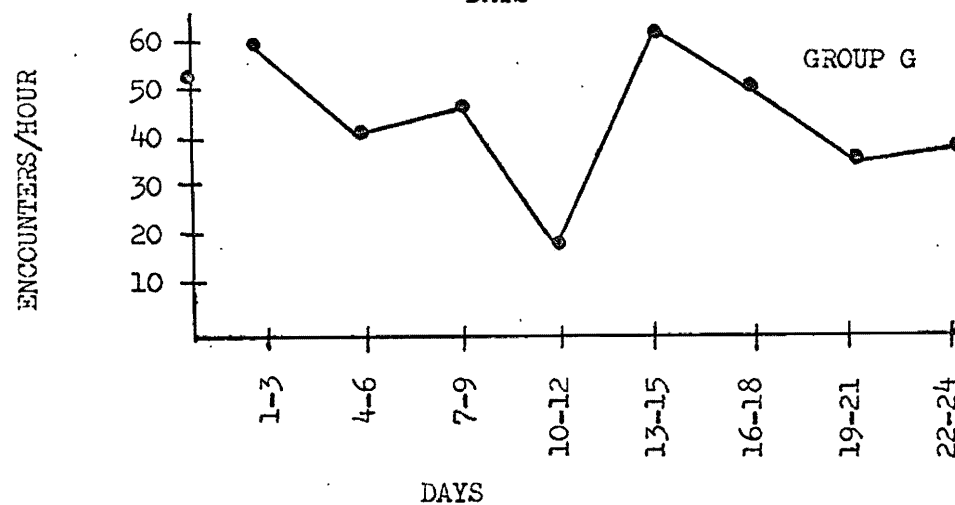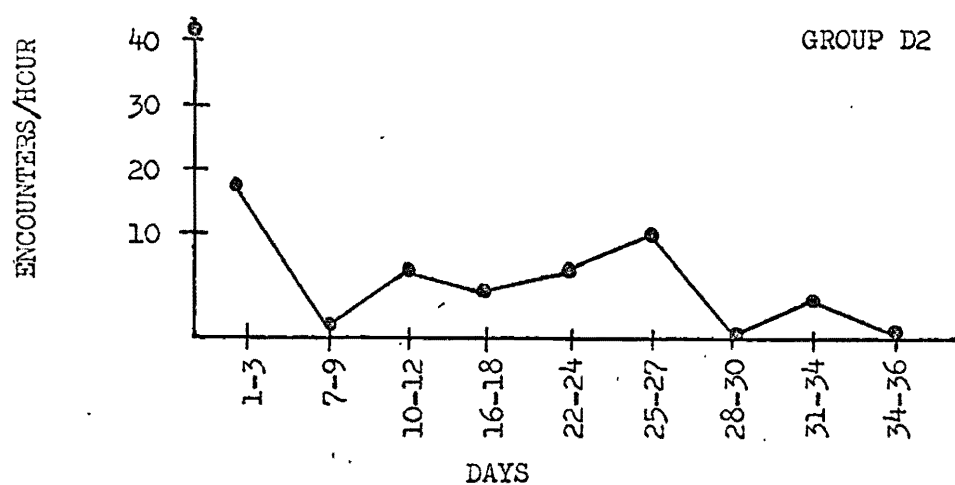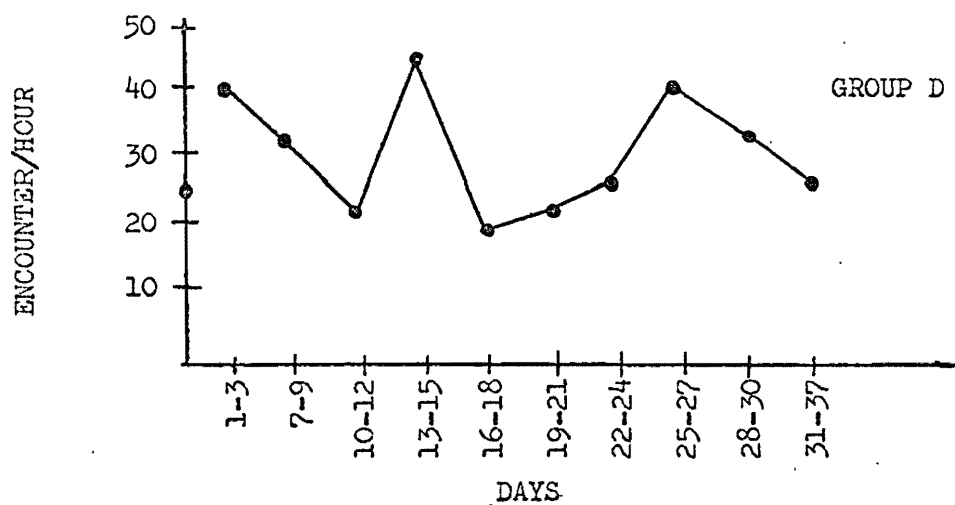
Figure 4. Frequency of agonistic encounters through time in three cage groups observed between October 9 and December 19,1972. The dot on the ordinate represents the encounter rate for the first day the group is together.

enough to produce a clear representation.

Cage A shows a general trend toward increased agonistic behavior, while groups B2 and C2 show a general decrease with time. Groups B, C, D, and G show fluctuating levels of agonistic encounters, but no trend either to decrease or increase. Groups A2 and D2 show an initially high rate of encounters (particularly emphatic when the first day's average is considered), followed by a sharp drop and subsequent relative stability at a low average frequency. Taking the agonistic behaviors in each interval from all the cages together, the curve somewhat resembles a normal extinction curve (Figure 5).

To reveal any changes in percentages of types of agonistic behaviors through time in each cage, threats, chases, displacements, and fights were separately tabulated in successive four or five day intervals. No significant change or trend was evident between initial and later intervals, with the number of threats remaining low, and chases remaining proportionally much higher.

IV SEASONAL VARIATION

Despite the tendency for E. townsendii to hibernate from late autumn to early spring (Walker 1923; Anthony 1924; Tevis 1966), my caged animals remained active throughout the study. Moreover, despite an un-
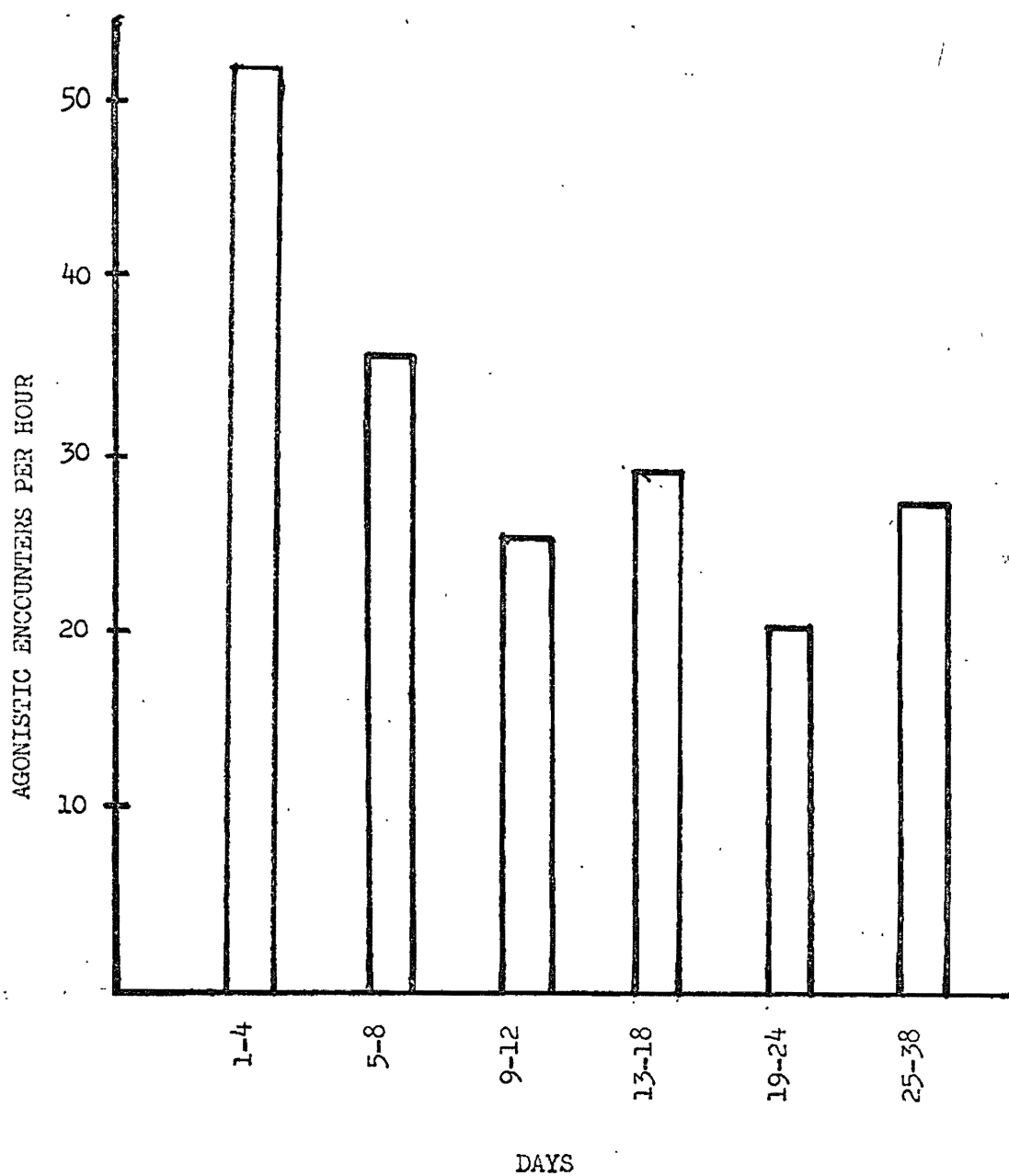
Figure 5. Total agonistic encounters in all cages during
successive time intervals

usually cold December when temperatures remained below freezing for two weeks and reached -5° to -10° C., the greatest frequency of agonistic encounters occurred in November and December. A graph showing the total number of agonistic encounters through time (Figure 6) suggests a general increase in agonistic encounters from August to December, with a peak in September surrounded by lower periods in August and October.

The lowest frequency of agonistic encounters was during August when temperatures averaged near 27° C. My results suggest a pattern of seasonal variation in agonistic encounters among the chipmunks in this study. Non-agonistic and agonistic behaviors combined averaged approximately 39 per hour in August in contrast to 47 for September, 49 for both October and November, and 52 for December.

Figure 7 shows variations in type of agonistic behaviors in my study, with each point on the curve representing the average over a 15-day period. A great number of threats occurred during August relative to later months. Only during the first month did threats approach the number of displacements, actually surpassing the latter during the first 15 days. Threat frequency diminished during September, and persisted at a relatively stable, low level for the remainder of the study. Fighting declined after August and remained at a low
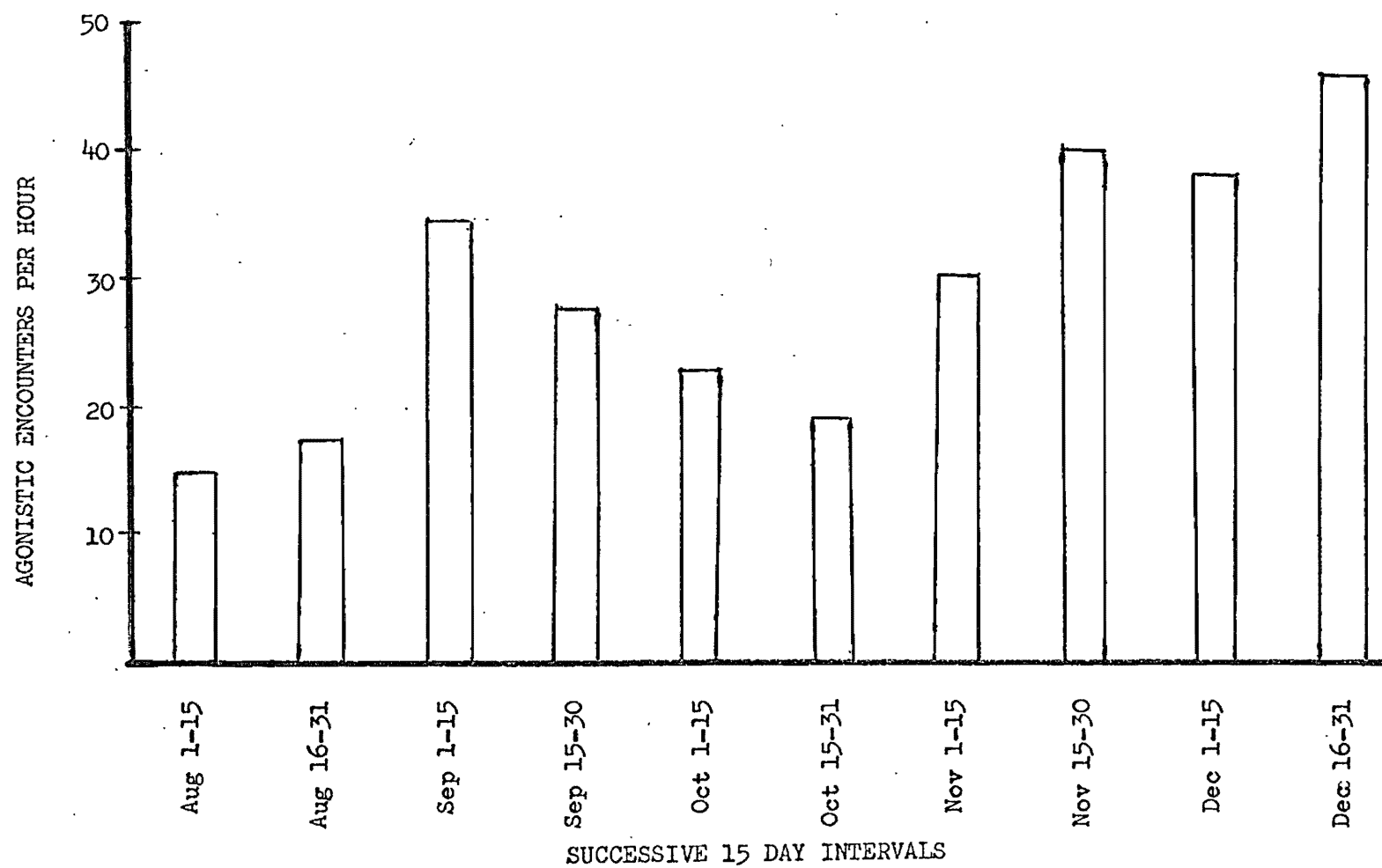
Figure 6. Seasonal variations in overall agonistic encounters (average encounters per hour in successive 15 day intervals).
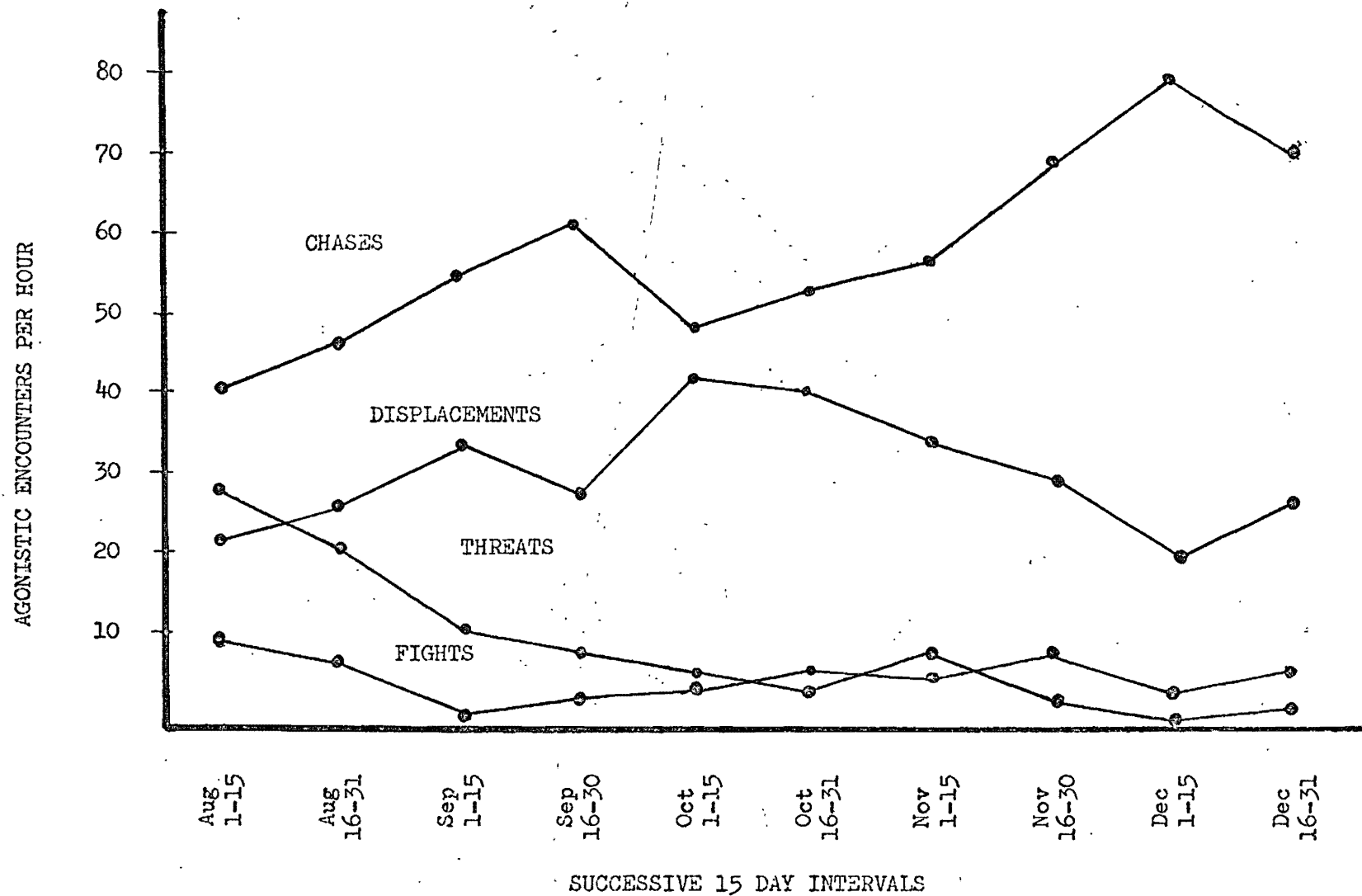
Figure 7. Seasonal variation in frequencies of four types of agonistic behaviors in Successive 15 day intervals.

level throughout the rest of the study. After an initial sharp rise in both chases and displacements, the two curves appear almost as mirror images of each other.

Groups A and H, observed during August and December respectively, contained the same combination of four chipmunks. In addition to two dominance changes mentioned earlier, agonistic behavior in December was considerably greater. Overall, the frequency of agonistic encounters more than doubled, from 21.9 per hour to 43.3. Non-agonistic behavior remained at comparable levels (17.8 and 23.4). The total intraspecific activity (frequency of all encounters) was 39.7 per hour in August and 66.7 in December. The change in types of agonistic behaviors was marked, with threats diminishing from 22.1% to 1.6% and chases increasing from 46.0% to 68.4%. Displacements and fights were similar in the two groups.

V INTERGROUP AND INDIVIDUAL VARIATION

Frequency of agonistic encounters varied a great deal among cage groups, even when observed during the same period (Figure 8). The range of frequencies of agonistic encounters in the 12 cage groups was 4.8 per hour to 43.9 per hour. The total average for the study was 28.0 agonistic encounters per hour (N=6441, T=230 hours). Frequencies of the four types of agonistic behavior also varied widely among individual cage groups.
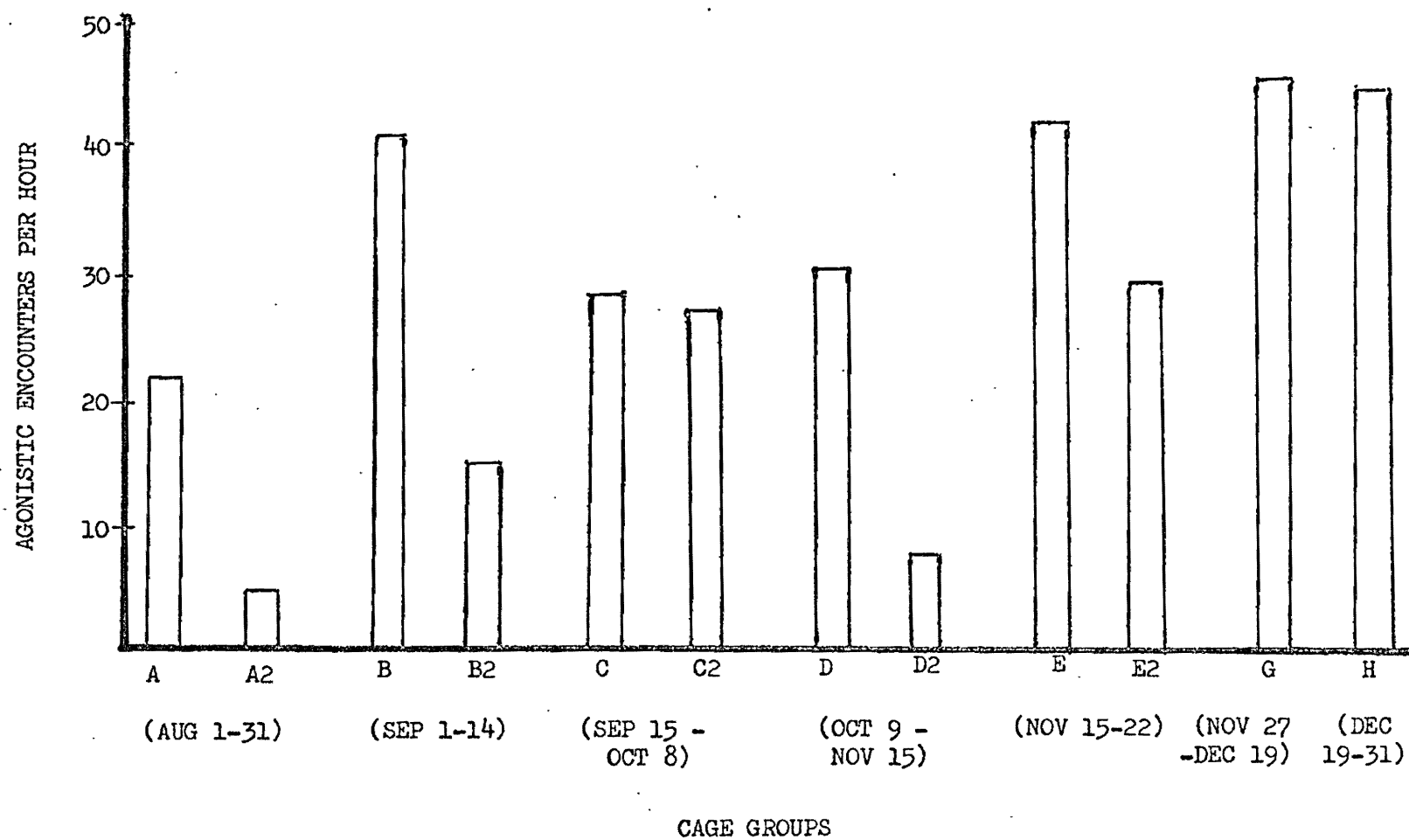
Figure 8. Frequency of agonistic encounters in 12 cage groups.

The chart shows AGONISTIC ENCOUNTERS PER HOUR (y-axis, scale 10 to 50) versus CAGE GROUPS (x-axis).

Cage groups with date ranges:
- A, A2 (AUG 1-31)
- B, B2 (SEP 1-14)
- C, C2 (SEP 15 - OCT 8)
- D, D2 (OCT 9 - NOV 15)
- E, E2 (NOV 15-22)
- G (NOV 27 -DEC 19)
- H (DEC 19-31)

Threats comprised from 0.9% to 31.3% of the total
agonistic encounters and chases from 31.3% to 73.5%.
Displacements made up between 14.9% and 40.1% of the
totals and fights between 0.6% and 23.4%.

Non-agonistic encounters tended to be higher in
groups with low agonistic behavior frequencies. The high-
est average number of non-agonistic encounters (47.7/hr.)
occurred in group D2, where only 7.8 agonistic encounters
per hour were recorded. The lowest frequency of non-agon-
istic encounters (1.8) was observed in group G, where
the highest frequency of agonistic behaviors occurred.
The possibility of high agonistic and non-agonistic behav-
iors occurring together is enhanced in a cage where both
tolerance and dominant-subordinate relationships exist.
This happened in group H where 25.4 non-agonistic encount-
ers per hour in addition to 43.9 agonistic encounters
produced a total rate of 66.7 per hour.

A great deal of individual variability in behavior
was apparent during the project. Some chipmunks were
clearly more aggressive than others. WH, the alpha
chipmunk in the study, was the least frequently observed
out of the nest box and least disposed to chase. In its
initial cage experience, WH showed tolerance toward two
conspecifics and chased the other only sparingly. RH, a
co-dominant in that cage, engaged in over 2.4 times as
many agonistic encounters. In its next group however,

WH recorded over twice as many agonistic behaviors in 25% less time.

WH was in some ways the most timid of the subjects, taking considerably longer to come out after a disturbance than the others. WT2 and O, on the other hand, were a good deal less timid than the others. WT2 approached me closely enough to eat from a held tin or knife, while even two months later, others still retreated hastily to the nest boxes when I approached the cage. O and WT2, curiously, occupied two of the three lowest positions in the hierarchy.

DISCUSSION

Although primarily solitary, chipmunks have widely
overlapping ranges and are found to aggregate in places
where local food supplies are abundant or preferred
(Gordon 1943; Yerger 1953; Dunford 1970). Thus, a domi-
nance hierarchy to minimize fighting and chasing would be
of selective advantage. Observations of E. townsendii
revealed the existence of a rapidly formed, stable hier-
archy. Figures 3 and 4 show that agonistic behaviors in
the various cage groups generally do not follow the
pattern of gradual extinction. Further, Figure 7 shows
that a transition from fighting and chasing to threat
and displacement is not realized. Threats were very few
and not highly stereotyped, perhaps due to the chipmunk's
relatively solitary existence, and consequently effective-
ness was inconsistent. A threat must be easily recognized
as such if it is to be effective. Although individual
recognition and memory are achieved, the escape and
avoidance drives are insufficient to reduce encounters to
a low level, and not appreciably intensified even by
repeated chases. Habituation for chasing did not occur
in relationships between some pairs.

My data suggest a number of possible explanations

for the selective advantage of dominance hierarchy in
chipmunks. First, the relatively rare occasions of
fighting compared to other patterns of agonistic behavior
is of some advantage (Figure 7). Visible injury never
occurred in the fights I observed, and field work
(Broadbooks 1958; Brand 1970) indicated that few serious
injuries occur in natural Eutamias populations. Toler-
ance or severely curtailed agonistic behavior, rather
than intense conflict, was manifested in equals. Only
in clear-cut dominance-subordinate relationships did a
great deal of agonistic behavior exist. Since these
encounters involved either chases or displacements, in
which escape was nearly certain, few serious confron-
tations arose. Escape in wild populations, particularly
with E. townsendii, which inhabit forested areas, is
almost ensured. Agonistic behavior of dominant chip-
munks is not confined or even focused on one member of
the hierarchy, often the top subordinate in other
animals, but is spread throughout, thus reducing intense
pair conflicts. Furthermore, the seeming inhibition of
fighting in Eutamias may be another check against physical
damage. Another advantageous consequence of dominance is
that the strongest and most fit animals have access to
preferred mates and locally short supplies of food. Ago-
nistic behavior in general also serves for dispersal,
protection of young, and population control (Sheppard and

Yoshida 1971; Broadbooks 1970; Steiner 1972).

Another function of agonistic behavior in _Eutamias_ is to competitively exclued other species in areas of overlap. Heller (1970) found that _E. amoenus_ and _E. alpinus_, by virtue of their more aggressive natures, exclude _E. speciosus_ and _E. minimus_ from areas included in the latter two animals' fundamental niches. The result is an altitudinal zonation of species. Brown(1971) and Sheppard (1971) found similar exclusions of less aggressive _Eutamias_ by more aggressive ones. Aggressive exclusion does not always occur, however. Broadbooks (1970) and Dalquest (1970) found _E. amoenus_ feeding alongside _E. minimus_ and _E. townsendii_ respectively. The chipmunks in my work are the only species of _Eutamias_ in the area.

The failure of chipmunks to avoid confrontations with dominants even after severe chasing has a selective advantage for subordinates, particularly where food is concerned. My study confirms other work (Fraleigh 1929; Wolfe 1966; Brand 1970) in asserting that food is the focal point of agonistic behavior in natural populations and its presence engenders aggression. Low-ranked individuals, dominated at a preferred food source, approach incessantly, regardless of intensity of chase or location. In caged _Eutamias_, only one feeding area was present, and subordinate approaches were common. Wolfe (1966) found that chasing did not reinforce the escape drive in

captive <u>Tamias</u> either. The most intense agonistic behavior is often associated with food.

Field studies show that hierarchies appear to be less stable in wild populations of chipmunks than in captive groups (Gordon 1943; Brand 1970; Dunford 1970). The primary reason for the instability is the disorganization that arises with the departure and arrival of different or new chipmunks in addition to the consistent presence of different combinations of individuals. My work indicates that both frequency of agonistic behavior and reversals of dominance are affected by establishing new groups. Brand (1970) stated that when a great number of chipmunks assembled, reversals were frequent. Presumably this was due to the inability to recognize individuals. In captive chipmunks, recognition plus stability of groups resulted in stability of hierarchy and infrequency of reversals.

Changing combinations of chipmunks in cages demonstrated concentrated aggression toward a new animal by the dominant, and a general increase in overall agonistic behavior including intensification in the established relationships among other chipmunks in the cage. Subordinate animals that were tolerated for weeks previously were suddenly chased vigorously. Animals such as WH were much more aggressive in some cage groups than in others. WH, for example, initiated an average of 5.2 agonistic

encounters in group A, then averaged 14.2 encounters in the next group (B) with only one change made. The make-up of the group, then, is important in determining the level of agonistic encounters. Figure 8 demonstrates the wide range of agonistic encounters in the 12 cage groups (4.7-43.9 per hour).

Seasonal variations, although much less a factor in level of agonistic behavior, may exist as indicated by Figure 6. Gordon (1943) and Yerger (1953) observed that the peak of agonistic behavior in wild *Tamias* occurred in late September and early October, declining thereafter. Brand (1970) reported a marked decrease in winter aggression among *Eutamias*, although the number of encounters did not decrease. Wolfe (1966) found a greatly reduced number of chases in *T. striatus* in July, and postulated a pattern of seasonal variation in that species. My results suggest a similar depression in overall agonistic behavior and activity during the late summer, followed by a peak period in September. Summer abundance of food and high temperatures, followed by increased drive to store quantities of a diminishing supply of food are likely involved in this pattern. The failure of my chipmunks to decrease activity or hibernate as winter approached was perhaps due to the artificially constant food supply or other results of captivity.

The existence and importance of individual differ-

ences in agonistic behavior of chipmunks was observed
both qualitatively and quantitatively in my study.
Broadbooks (1958) asserted that individual differences in
temperament of young E. amoenus were marked by the end
of the first month. Fraleigh (1929), Gordon (1943), and
others have reported an extreme variability in timidity,
activity, aggressiveness, and temperament in other species
of chipmunks. Although size appears to be the best
physical determinant of rank, it is supplanted repeat-
edly by individuality. Causes for this may be different
thresholds for eliciting agonistic behavior, variations
in endocrine output, genetic variations, age, and past
experience. The relative importance of experience in
determining rank or aggressiveness is unknown in natural
populations, but captive E. townsendii show a consider-
able effect of conditioning. This is exemplified by many
instances in which a dominant-subordinate relationship
is established without prior conflict, with the dominant
assuming the role of chaser and the subordinate taking the
opposite role. Extinction of the escape drive in very low
ranking chipmunks is very slow.

Despite the general persistence of agonistic behav-
iors, such interactions between some pairs decreased to
the point of infrequency or extinction. Subsequent
encounters between these animals were predominantly recog-
nitory or sexual. In most interactions following this

pattern, conflicts waned within three days. Others persisted several more days at a high level before dropping appreciably. An increase in agonistic encounters with time was also observed in a number of pair relationships. Individual recognition is the key to establishment of a dominance hierarchy. It has been mentioned before that some subordinates are not chased at all, while others are chased consistently and vigorously. The great number of displacements recorded indicates recognition to the point of awareness of rank with respect to an approaching chipmunk. The response to the approach of an equal, tolerant dominant, or subordinate is quite distinct from response to an aggressive dominant. The consistency of dominant victories (99.3%) relates in part to the efficiency of the mechanism for recognition. A behavior often recorded was the continuation of a dominant's chase from a subordinate normally harassed to one who was rarely, if ever, chased under other circumstances. In most of these instances, the dominant merely chased the tolerated chipmunk a few feet, and frequently touched noses immediately. A number of times, a dominant who started to chase a tolerated conspecific stopped abruptly as if the chased animal was then recognized. Regarding dominant-subordinate relationships in general, the proximity of another animal was not always a sufficient stimulus for agonistic behavior, nor was a particular

size, sex, or rank.

Lack of quantitative studies limits comparison of the structure and development of agonistic behavior in E. townsendii to those in other sciurids, but dominance hierarchies, with the exception of Cynomys, are similar in generally lacking strict linearity in natural populations, in demonstrating relative stability and infrequent reversals, and in using avoidance or escape as primary methods of minimizing injurious encounters. Agonistic behavior in the family Sciuridae varies from Spermophilus columbianus(Steiner 1972) and S. townsendii (Alcorn 1940), in which severe injuries and fights occur often, to Glaucomys sabrinus which is highly sociable (Burt 1940). Dominance hierarchies range from virtual absence in highly territorial sciurids where physical contact is rare, such as Tamiasciurus (Smith 1968) and S. fremontii (Gordon 1936), to the well-defined and peaceful hierarchy of Cynomys (King 1951 and Anthony 1955). Stereotypy and ritualization are much more developed in Cynomys and many ground squirrels than in chipmunks (Sheppard and Yoshida 1971; Yeaton 1972) or in genus Marmota (Bronson 1964; Armitage 1965). Although my chipmunks groomed meticuously and persistently, no social grooming was apparent. Appeasement behaviors, relatively common in other sciurids (King 1951; Bronson 1964; Steiner 1972; Yeaton 1972), were undeveloped in E. townsendii, presumably because

escape and avoidance are employed almost exclusively in natural populations to regulate aggression. I reported several appeasement behaviors in captive chipmunks, but their use was sporatic and their effectiveness marginal.

Although the similarity between Eutamias and Tamias is marked, several differences occur in comparing the two genera. The intensity of agonistic encounters and occurrences of wounds and mortality due to fighting is much less (absent in my work) in E. townsendii (Dalquest 1948). Broadbooks (1970) observed repeated fighting and chasing in E. amoenus without fatalities. Interspecific fighting among Eutamias species was usually brief in the field, but often more severe in the lab (Brand 1970). Wolfe (1966) reported 11 mortalities and several other crippling injuries due to fighting in caged Tamias, and Condrin (1936) observed "invariable death" when two T. striatus were confined together. Subordinate E. townsendii engage in considerably more agonistic encounters, and chases by dominants are spread out over the entire hierarchy more evenly. Wolfe (1966) correlated higher numbers of encounters with closeness of rank in Tamias, and found a correlation between rank and number of agonistic behaviors participated in. Neither were the case in my study. Subordinate victories occurred with four times the frequency (3.1%) in Wolfe's (1966) study of Tamias.

Patterns of agonistic behavior, hierarchy structure, and overall frequency of types of agonistic behavior were highly comparable in eastern and western chipmunks. Chases were the most common agonistic behavior in captive _Tamias_ (Wolfe 1966; Dunford 1970) as in my _Eutamias_, and made up a percentage of total observed agonistic behaviors comparable to that in my study. The percentage in Brand's (1970) study of _Eutamias_ was also similar. Fighting in captive _Tamias_ (Yerger 1953; Wolfe 1966) was more frequent than in my study, but began and ended similarly. Comparable threats were also reported for _Tamias_ and for other species of _Eutamias_ (Brand 1970).

Further study of agonistic behavior and dominance in western chipmunks would perhaps be most beneficial in the area of quantitative field work with natural populations to augment the present study on captive animals. In addition, comparative studies of the 16 species of _Eutamias_, relating social behavior to habitat, range, and other natural history information, would delineate more clearly the ecological significance and developmental history of dominance and agonistic behavior in the genus.

CONCLUSIONS

1. Dominance hierarchies in <u>E. townsendii</u> are not effective in substantially abating agonistic behavior.

2. Initiation of agonistic behavior is affected by a combination of factors including hunger, season, individual differences in disposition, the presence of unknown animals, disorganization of the hierarchy, and (perhaps most importantly) the reaction of the subordinate.

3. Experience and individual differences in activity and aggressiveness are more important determinants of rank than either sex or size.

4. Residence is of no significance in intraspecific encounters among chipmunks.

5. Food is the focal point of agonistic behavior and its presence engenders aggression.

6. Repetitive chasing did not reinforce the escape drive in subordinate chipmunks.

7. Disorganization of a hierarchy and unfamiliarity results in an increase in agonistic behavior and in reversals of dominance. Extreme hierarchical and dominance stability is a result of recognition within a stable

group.

8. Dominance in E. townsendii, although ineffective in reducing time and energy losses through chasing, offers a selective advantage by curtailing serious confrontations, and in some cases enhancing the establishment of tolerance between individuals.

REFERENCES

Ackerman, R. and P.D. Weigel. 1970. Dominance Relations of Red and Grey Squirrels. Ecology, 51: 332-334.

Alcorn, J.R. 1940. Life History Notes of Piute Ground Squirrel. J. Mamm., 21: 160-170.

Anthony, A. 1955. Behavioral Patterns in a Laboratory Colony of Prairie Dogs, Cynomys ludovicianus. J. Mamm., 36: 69-78.

Anthony, A.W. 1924. Hibernating Chipmunks. J. Mamm., 5: 76.

Armitage, K. 1965. Vernal Behavior of the Yellow Bellied Marmot (Marmota flaviventris). Animal Behav., 13: 59-68.

Balph, D.F. and A.W. Stokes. 1963. On the Ethology of a Population of Uinta Ground Squirrels. Amer. Midland Nat., 69: 106-126.

Brand, L.R. 1970. Vocalizations and Behavior of Chipmunks in California. Ph. D. Thesis, Cornell Univ., 128 pp.

Broadbooks, H.E. 1958. Life History and Ecology of the Chipmunk, Eutamias amoenus in Eastern Washington. Misc. Publ. in Zool., Univ. of Michigan, no. 103, 42 pp.

Broadbooks, H.E. 1970a. Home Range and Territorial Behavior of the Yellow-Pine Chipmunk, Eutamias amoenus. J. Mamm., 51: 310-326.

Broadbooks, H.E. 1970b. Populations of the Yellow-Pine Chipmunk (Eutamias amoenus). Amer. Midland Nat., 83: 472-488.

Bronson, F.H. 1964. Agonistic Behavior in Woodchucks. Animal Behav., 12: 470-478.

Brown, J.H. 1971. Mechanisms of Competitive Exclusion Between Two Species of Chipmunks. Ecology, 52: 305-311.

Burt, W.H. 1940. Territorial Behavior in Populations of Small Mammals in Southern Michigan. Misc. Publ. Mus. Zool., Univ. of Mich., no. 45, 58 pp.

Carl, E.A. 1971. Population Control in Arctic Ground Squirrels. Ecology, 52: 395-413.

Condrin, J.M. 1936. Observations of Seasonal and Reproductive Activity of Eastern Chipmunks. J. Mamm., 17: 231-234.

Dalquest, W.W. 1948. Mammals of Washington. Univ. of Kansas publ. Mus. of Natural History, Lawrence, Kansas, 2: 444 pp.

Dunford, C. 1970. Behavior Aspects of Spatial Organization in the Chipmunk, Tamias striatus. Behavior, 36: 215-231.

Farentinos, R.C. 1972. Social Dominance and Mating Activity in the Tassel-Eared Squirrel (Sciurus aberti ferreus). Animal Behav., 20: 316-326.

Forbes, R.B. and L. Turner. 1972. Notes on Two Litters of Townsend's Chipmunks. J. Mamm., 53: 355-359.

Fraleigh, L.B. 1929. The Habits of Mammals at an Adirondack Camp. N.Y. State Mus. Handbook, no. 8: 119-167.

Gordon, K. 1936. Territorial Behavior and Social Dominance among Sciuridae. J. Mamm., 17: 171-72.

Gordon, K. 1938. Observations of the Behavior of Callospermophilus and Eutamias. J. Mamm., 19: 78-84.

Gordon, K. 1943. The Natural History and Behavior of the Western Chipmunk and the Mantled Ground Squirrel. Oregon State Monographs in Zool., 5: 1-104.

Heller, Horace. 1970. Altitudinal Zonation of Chipmunks: Interspecific Aggression, Water Balance, and Energy Budgets. Ph.D. Thesis, Yale Univ., 112 pp.

Howell, H.H. 1929. Revision of the American Chipmunks. North American Fauna, no. 52: 1-157.

Kilham, L. 1954. Territorial Behavior of the Red Squirrel. J. Mamm., 35: 252-253.

King, J.A. 1951. Social Behavior, Social Organization, and Population Dynamics in a Black-Tailed Prairie Dog Town in the Black Hills of S. Dakota. Ph.D. Thesis, Univ. Of Mich., 329 pp.

Meredith, D.H. 1972. Subalpine Cover Associations of Eutamias amoenus and Eutamias townsendii in the Washington Cascades. Amer. Midland Nat., 88: 348-357.

Peck, J.C. 1967. Influence of Social Hierarchy on Gray Squirrel Behavior. J. Wildlife Mgmt. 31: 720-728.

Quanstrom, W.R. 1971. Behavior of Richardson's Ground Squirrel. Animal Behav., 19: 646-652.

Reilly, R.E. 1972. Pseudo-Copulatory Behavior in Eutamias minimus in an Enclosure. Amer. Midland Nat., 88: 232.

Sheppard, D.H. 1971. Competition Between Two Chipmunk Species (Eutamias), Ecology, 52: 320-329.

Sheppard, D.H. and S.M. Yoshida. 1971. Social Behavior in Captive Richardson's Ground Squirrels. J. Mamm., 52: 793-799.

Smith, C.C. 1968. The Adaptive Nature of Social Organization in the genus of Tree Squirrels (Tamiasciurus). Ecological Monog., 38: 31-62.

Steiner, A.L. 1972. Mortality Resulting from Intraspecific Fighting in some Ground Squirrel Populations. J. Mamm., 53: 601-603.

Taylor, J.C. 1966. Home Range and Agonistic Behavior in the Grey Squirrel. Symp. Zool. Soc. Lond., 18: 229-235.

Tevis, L. 1956. Responses of Small Mammal Populations to Logging in Douglas-fir Forests. J. Mamm., 37: 189-196.

Tinbergen, N. 1965. Social Behavior in Animals. Wiley and Sons, NY., 150 pp.

Walker, A. 1923. Notes on the Winter Habits of Eutamias townsendii. J. Mamm., 4: 257.

Warner, G.M. 1971. Vocalizations of the Townsend Chipmunk (Eutamias townsendii). M.S. Thesis, Portland State Univ., 37 pp.

Wolfe, J.L. 1966. Agonistic Behavior and Dominance
Relationships of Eastern Chipmunk, _Tamias striatus_.
Amer. Midland Nat., 76: 190-200.

Yeaton, R.I. 1972. Social Behavior and Social Organiza-
tion in Richardson's Ground Squirrel (_Spermophilus
richardsonii_) in Saskatchewan. J. Mamm., 53:
139-147.

Yerger, R.W. 1953. Home Range, Territoriality, and
Populations of the Chipmunk in Central New York.
J. Mamm., 34: 448-458.