Behav. Ecol. Sociobiol. 3, 397–427 (1978)

Behavioral Ecology and Sociobiology
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The Adaptive Nature of the Social System and Behavior in the Eastern Chipmunk, *Tamias striatus*

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Received October 4, 1977

Summary. 1. The social system and behavior of a population of *Tamias striatus* were studied from October 1973 to November 1976 on a 5-ha woodlot in southeastern Ohio. The basic social unit is the solitary individual occupying a single burrow system, but a more complex social unit consisting of mother and litter persists briefly until emergence and dispersal of the litter from the natal burrow site. Burrow systems are distributed in a regular pattern and are surrounded by nonoverlapping core areas which are defended throughout the year by adults and seldom by subadults or juveniles. Defense of home sites has evolved as a mechanism to insure individuals an adequate share of a seasonal food supply. Two other spacing mechanisms occur in the annual cycle: defense of individual distances and relative dominance hierarchies. Rare instances of aggressive behavior in juveniles and subadults are examples of defense of individual distance. Relative dominance hierarchies form among adult males participating in a mating bout in core areas of estrous females. Brief pairing and multiple mating occur during a single mating bout.

2. Time budgets vary with sex and age class and also due to temporal, spatial, and social factors. The adaptiveness of differential time budgets resulting from the effects of these factors is discussed. Individual behavioral profiles are related to successful defense of home sites and reproductive fitness. Unaggressive adults are never or rarely territorial and do not mate, but extreme aggressiveness may be disadvantageous under certain circumstances. The ontogeny of aggressive behavior is discussed and factors selecting against precocious aggressiveness and sexual behavior are suggested.

3. The social system and behavior are major determinants of population dynamics and spatial distribution. Territoriality acts to regulate population

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density and partially determines the pattern of dispersion. Dispersing juveniles are forced into vacant areas, marginal habitats, or distant areas from birth sites by aggressive behavior in residents. Extrinsic factors which regulate density and determine spatial distribution include food resources and predation. The social system and behavior typifies that of a mammalian species adapted to a dispersed, solitary way of life.

Introduction

A social system is based on all behavioral interactions among members of a group or species and is a product of individual and kin selection (Smith, 1968; West Eberhard, 1975). The structure and dynamics of a social system can be described by an analysis of the mating, rearing, resource-exploitation, and predator-avoidance components of that system (Crook et al., 1976). Ecological factors and social behavior are major determinants in the evolution of the structure of a particular social system (Crook, 1970; Brown, 1975). A colonial social structure is generally adaptive when extended pair bonds are formed, young mature slowly, effective use of localized and abundant food resources necessitates tolerance of conspecifics, and predator detection is facilitated in social units occupying open terrain. In a solitary social structure, duration of pair bonds is brief, young mature rapidly, food resources are dispersed, and individual defense of home sites insures optimal use of resources with minimum expenditure of energy (Eisenberg, 1966; Smith, 1968; Barash, 1974; Crook et al., 1976).

Species of the family *Sciuridae* exhibit a continuum of social structure. Several tree squirrels (*Sciurus aberti*, Farentinos, 1974; *Tamiasciurus* spp., Smith, 1968) and ground squirrels (*Marmota monax*, Davis et al., 1964; *Spermophilus franklinii*, Kivett et al., 1976; *Eutamias amoenus*, Heller, 1971) are solitary except during the breeding season. Variable degrees of more complex structure are common to other sciurids (*Marmota flaviventris*, Armitage, 1962; Svendsen, 1974; *Cynomys ludovicianus*, King, 1955; *Spermophilus columbianus*, Kivett et al., 1976).

The eastern chipmunk, *Tamias striatus*, is a diurnal, semifossorial sciurid common to eastern North America (Hall and Kelson, 1959). Dunford (1970) and Elliot (in press) concluded that the eastern chipmunk is territorial based on the evidence that each animal is dominant around its burrow system. They noted that the area of dominance approximates the core area which does not overlap those of neighbors, whereas other sectors of home ranges overlap almost entirely. Many aspects of the life history of *Tamias* have been reported (see Forbes, 1966 for review), and those of Wolfe (1966, 1969), Dunford (1970), Ickes (1974), and Elliot (in press), have investigated the behavior and social organization of the species.

The present study is a comprehensive, long-term investigation of *Tamias* socioecology and is designed to determine the adaptive nature of the social system and behavior. Three major hypotheses are tested: (1) there is no change in the social system over season, (2) behavior does not vary with age or sex class nor with temporal, spatial, or social factors, and (3) the social system and social behavior have no effect on spatial distribution and population dynamics.

Materials and Methods

1. Study Area and Field Techniques

A population of eastern chipmunks was studied from October 1973 to November 1976 on a 5-ha deciduous woodlot located 5.9 km south of Athens, Athens Co., Ohio. The study area contains two major habitats: a northwestern sector uninhabited by chipmunks (1.5 ha), characterized by dense understory, abundant herbaceous growth, and few mast-producing trees, and a sector inhabited by chipmunks (3.5 ha), containing relatively sparse understory and herbaceous growth and numerous trees producing late summer and autumn mast crops. Cattle periodically graze in the latter sector. Three small streams traverse the woodlot. Extensive pastures and hayfields surround 95% of the plot boundaries and isolate the study area from other woodlots. Svendsen and Yahner (in press) describe other physiographic, topographic, and vegetative features of the study area.

Field observations and livetrapping totaling 2500 h began each year prior to the winter breeding season (early February) and continued until all animals terminated surface activity and presumably began periods of torpor (mid-November). Periodic observations were made from mid-November to early February to confirm above-ground inactivity. I regularly visited the study area (4–7 days per week) during different times of the day (2–12 h per day) to insure that all portions of the annual and diurnal cycle (early February to mid-November) received adequate study. Sixty National live traps, baited with sunflower seeds, were placed at least 2 days per week near entrances of occupied burrow systems and in localities used by chipmunks in daily activities. One hundred and eighty chipmunks were marked with numbered ear tags (#1, National Band and Tag Co.) and individual patterns of fur dye (Nyansol D). Sex, age, weight, and reproductive condition were noted at each capture. Age classes were designated as juvenile (<5 months), subadult (5–10 months), and adult (>10 months). Spring-born and summer-born juveniles were separated by this classification, but no juvenile class exists in the breeding season because the time from birth of litters to the subsequent breeding season exceeds 4 months. Thus, chipmunks were grouped as adult and young (≤ 10 months) when seasonal trends in behavior were analyzed.

The annual cycle of chipmunk activity was divided into three periods: breeding season, mid-February to early March (winter breeding season) and again in July (summer breeding season); spring, mid-March to late June; and autumn, August to mid-November. Three diurnal periods were recognized: morning, sunrise to 1000 h; midday, 1000 to 1400 h; and evening, 1400 h to sunset (EST).

The pattern of dispersion was determined by recording the location of burrow systems used by resident animals in the 3.5-ha sector during early June and early September of each year. These periods were selected to avoid temporary annual peaks in population densities due to juvenile dispersal. The 3.5-ha sector was divided into twelve 0.3-ha quadrats, and the number of burrow systems per quadrat was recorded in each of the two months. Results for the 3 years were then pooled. A variance/mean ratio was calculated and compared to the Poisson distribution by testing for deviation from 1.0 (Cox, 1976).

Behavioral observations were primarily confined to a 1.75-ha sector inhabited by 5 to 10 residents per ha during the study. I used the focal-area sampling technique (Altmann, 1974). Different portions of the sector were observed from specific locations ($N = 15$), which minimized detection of the observer but permitted sufficient fields of view to monitor areas used by chipmunks in daily activities. A location was randomly chosen every 20 min, and the surrounding area was scanned for activity. More time was spent at a location if a chipmunk remained in view beyond the time limit. Sex, age, position relative to the home site (within or outside the core area), and absence or presence of a conspecific (conspecific within 10 m of a specific animal) were noted for each animal sighted. Behavioral categories of the nearest animal, recorded with 7 × 35 field glasses and a portable cassette recorder, comprised an observation bout, which is defined as a sampling period beginning

Table 1. Descriptions and symbols for behavioral categories in the eastern chipmunk

Behavioral categories	Description
Pause (P)	Body remains motionless except for an occasional head movement or slight shift in position; all four feet touch substratum or forelegs may be elevated with back slightly arched; probably a continuum of motivational states ranging from true alert to rest
Vertical pause (V)	Same as Pause except only the hindlegs touch substratum; body oriented in an upright position perpendicular to substratum
Forage (F)	Traversing movements at a slow to moderate speed; head held close to substratum in a food-searching manner; includes digging with forelegs in leaf litter, soil, or rotten logs
Locomotion (L)	Traversing movements at a slow to moderate speed; head held above anterior-posterior plane of body
Run (R)	Same as Locomotion but speed of movement is rapid and tail is raised in a vertical position
Climb (CB)	Movement along a vertical object which is more than 2-m high
Drink (D)	Consumption of water
Eat (E)	Handling of a food item with forepaws and consumption
Collect leaf (CL)	Gathering a leaf from litter and using forepaws to manipulate it into mouth and cheek pouches (leaf is later taken into burrow system as nesting material)
Collect food (CF)	Using forepaws to gather and manipulate a food item into mouth and cheek pouches (includes only collection of food which is later scatter or larder hoarded)
Scatter hoard (SH)	Digging a depression in loose soil with forepaws, placing a food item in the depression, and covering item with soil and leaf litter using nose and forepaws (Yahner, 1975) (larder hoarding is not quantified because this method of hoarding involves transporting a food item into a burrow system out of view of the observer; placement of food into cheek pouches is considered Collect Food and actual transport to burrow system is Locomotion)
Scratch (S)	Scratching various areas of body with hind feet
Groom (G)	Only self-grooming occurs; various areas of the body, except head region, are licked with tongue or nibbled gently with incisors; forepaws are often licked and then rubbed over the facial and head region with anteriorly-directed motions
Locomotion-sniff (LSN)	Traversing movements at a moderate speed to slow, deliverate pace; nose held close to substratum while sniffing, and tail is sometimes held in a vertical position and vibrated rapidly; occurs only in adult males during the breeding season
Play (PL)	Observed in juvenile littermates prior to dispersal; includes mock fights, chases, nudging, mounting, and naso-nasal and naso-anal contacts
Agonistic behavior (AG)	Refers to any combative behavior involving a struggle or contest between conspecifics (King, 1973); includes total duration and frequency of five components: Threat, Chasing, Being Chased, Withdraw, and Fight

Table 1 (continued)

Behavioral categories	Description
Threat (T)	Described by Dunford (1970) and termed freezing and fixating in his study; entire body becomes completely immobile and eyes are wide open and fixed on a conspecific
Chasing (CG)	Attack and rapid movement directed toward an opponent driving it some distance from the immediate area
Being chased (CD)	Rapid movements away from an opponent delivering an attack
Withdraw (W)	Movement away from an area occupied by an opponent (within 2 m distant) without being driven away by an attack and chase
Fight (FT)	Two animals come together, lock into a 'ball,' and roll and tumble; each animal attempts to bite the head and shoulder regions of the opponent

with the initial recorded category and terminating with the last category observed to completion prior to losing sight of the animal. Because the length of observation bouts varied, comparison per unit time was the obvious solution to equate bouts of different length (see Altmann, 1974). Therefore, I converted duration (total seconds) and frequency (number of times performed) of each behavioral category recorded in an individual observation bout to two types of rate measurements (s/min and number of times performed/min), hereafter simply termed duration and frequency, by division of the total length of an individual bout (min) in order to standardize bouts of unequal length for comparative purposes. Actual recorded behavior totaled 150 h and consisted of 1279 bouts ranging in length from 1 to 45 min ($\bar{X} = 7$ min).

2. *Description of Behavioral Categories*

Twenty-one behavioral categories were distinguished (Table 1). Duration and frequency of copulation were not calculated because copulation usually occurred in localities where careful observation was impossible due to poor light conditions or presence of obstructions. Copulation is described and quantified in detail in a later section (see Mating System in Results).

3. *Analyses of Observation Bouts*

Total time budgets were determined by calculating mean duration and frequency of each behavioral category ($N = 1279$ bouts). These values were then converted to percentages.

Two sets of 4-way multivariate analyses of variance (manovas) (Finn, 1968) were performed on all bouts to determine how time budgets vary among levels of each factor or among levels of two or more factors considered simultaneously. In each set, durations of the 21 behavioral categories were analyzed separately from frequencies because of limitations in the design of the computer program. The six factors considered were: (1) sex class, (2) age class, (3) spatial factor: bout performed within or outside the core area, (4) social factor: conspecific absent or present (conspecific within an arbitrary distance of 10 m), and temporal factors including (5) annual-period factor: breeding season, spring, or autumn, and (6) diurnal-period factor: morning, midday, or evening. Sex class was included as one of the four factors in both sets of manovas. In the first set, age class (adult and young) and temporal factors (annual and diurnal periods) comprised the second, third, and fourth factors; in the second set, temporal factors were replaced with spatial and social factors, and age class (adult, subadult, and juvenile) was the remaining factor. Multivariate F-ratios tested the equality of mean vectors among levels of a factor or combination of factors. If the ratio were significant ($P<0.05$), univariate F-ratios, computed for individual behavioral categories, were inspected to determine which categories contributed significantly ($P<0.05$) to the discrimination among levels (Cooley and Lohnes, 1971). When a particular category was significant and the levels within a factor(s) exceeded two, levels were tested *a posteriori* using the Student-Newman-Keuls test (Sokal and Rohlf, 1969).

Social behavior of 25 chipmunks was examined using a Q-factor analysis. Observation bouts recorded in the presence of a conspecific during spring and autumn were included in the analysis. Mean durations and frequencies of 20 behavioral categories were calculated from bouts meeting these criteria for each individual of a particular age class (adult, subadult, or juvenile). Breeding season bouts were omitted because the social structure was altered appreciably in this season (see Mating System in Results). Locomotion-sniff was excluded from the analysis because it occurred only in the breeding season. Therefore, the original data matrix consisted of 40 rows (duration and frequency of 20 hehavioral categories) and 31 columns (5 chipmunks represented in more than one age class). Oblimin rotation of the factor matrix was performed, and factors were extracted by eigenvalues above 1.0 (Rummel. 1970).

Results

1. Seasonal Activity and Population Dynamics

Adult males began regular surface activity in mid-February several days prior to breeding adult females. Activity of adult males was restricted to short, early morning excursions (<50 m from burrow systems), and sexual behavior was exhibited when estrous females were encountered. If no estrous females were active, males soon returned to their burrow systems and remained underground until the following morning or several mornings thereafter. Activity of each breeding female, in contrast, was usually restricted to a single day coinciding with the date of peak estrus. Nonbreeding adult females and young of either sex were rarely active at this time of the year.

Chipmunks ceased above-ground activity after the winter breeding season, and surface activity resumed sometime between late March and mid-April depending on ambient temperatures (Yahner and Svendsen, 1978). Lactating females and small chipmunks (<85 g) typically resumed activity earlier than other individuals. In some cases, adult males did not become active above ground until late May.

A summer breeding season occurred in July. Subsequent to this, population activity decreased for several weeks (referred to as a summer lull; Dunford, 1972) and only small individuals maintained high levels of surface activity (Yahner, 1977a). Population activity increased progressively in late summer and chipmunks prepared food caches in late autumn prior to torpor. Adults and subadults commenced torpor by late October but juveniles remained active for 1 or 2 weeks longer.

Both numbers of individuals and age- and sex-class composition of the populations varied among years and with season (Fig. 1). Winter mortality during hibernation was the most plausible factor causing year-to-year variation in numbers. Four animals dies in trap accidents. Both predation and dispersal were probable causes of seasonal fluctuations in numbers. Predators, including

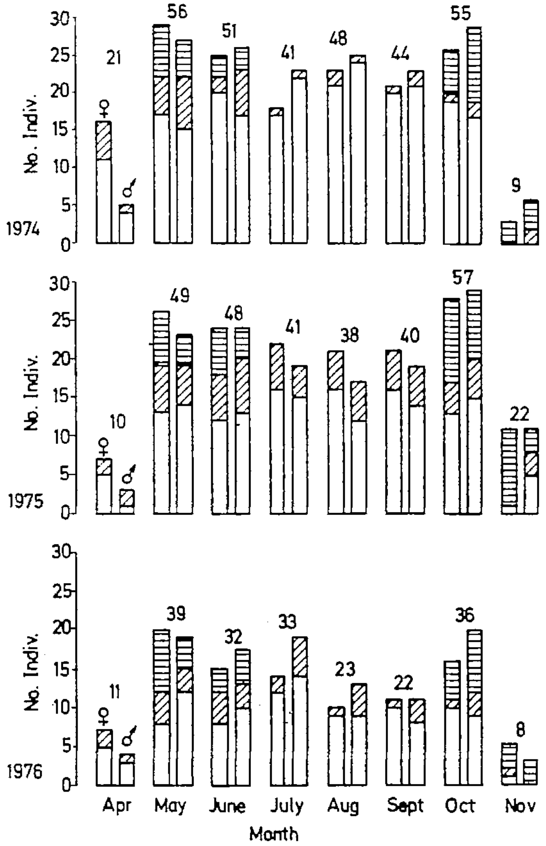

Fig. 1. Number of chipmunks by age and sex class occupying the 3.5-ha sector of the study area in southeastern Ohio during three consecutive years (1974–1976). *Open bar*, adult; *slash bar*, subadult; *stippled bar*, juvenile

long-tailed weasel *(Mustela frenata)*, house cat *(Felis domesticus)*, and Cooper's hawk *(Accipiter cooperii)*, were observed pursuing chipmunks and may have removed an important segment of the population. Peak annual densities varied from 11 animals/ha in 1976 to 16/ha in 1974 and occurred in May and October when spring and summer litters dispersed from natal burrow systems during an approximate 2-week period. About one-third of native-born juveniles established residency in the study area; others either dispersed to unknown areas or become prey in the process. No native-born juveniles were captured in surrounding woodlots during limited trapping attempts, but a few unmarked juveniles assumed to be born elsewhere immigrated to the study area each year and sometimes remained as residents. In short, numbers of young fluctuated appreciably with season whereas numbers of adults varied little. Low population densities in April and November resulted from differences in the onset and termination of torpid periods among resident chipmunks (see Yahner and Svendsen, 1978).

2. *Social Organization and Pattern of Dispersion*

Social structure during the nonbreeding season consisted of solitary individuals occupying separate burrow systems. Sociality and multiple occupancy of the same burrow system occurred only with the formation of small social units by mother and young, which persisted until dispersal of young from natal sites. Most seasonal activity was confined to small core areas (approximately ≤ 15 m in radius) surrounding burrow systems. Mean distance between neighboring burrow systems ($N = 132$) *was* 34.8 m. Dispersion of these systems tended toward a regular distribution (variance/mean ratio $= 0.59$, $t = -3.31$, $P < 0.001$).

3. *Spacing Mechanisms*

Three mechanisms of spacing were evident during the annual cycle: territoriality, defense of individual distance, and relative dominance hierarchies. A territory can be defined as a fixed, exclusive area maintained by aggressive behavior (Brown, 1975); thus, core areas of adults were considered territories although neighbors occasionally used these areas when residents were absent. Adult chipmunks within personal core areas were dominant and evicted all trespassers with threats and chases throughout the year.

Defense of core areas was specific to age class. With one exception, all 'older' adults (>12 months) were territorial, and most 'transitional' adults (11–12 months) excluded conspecifics from core areas. Territoriality occurred only once in subadults and never in juveniles. Young chipmunks (subadults and juveniles) typically tolerated or avoided conspecifics that infringed upon their core areas; often the trespasser chased the young resident. On rare occasions, the younger resident attacked an older intruder but never successfully forced it from the area; instead, the older animal subsequently attacked the younger resident. However, if the intruder and the resident were both young animals, reciprocal chases sometimes occurred. This reversal in the outcome of encounters was never observed in comparable situations involving two adults. Ten attacks by resident juveniles and subadults were recorded; six were initiated outside their core areas.

Dominance hierarchies were established among adult males during mating bouts. In each bout, one or two males clearly dominated most rivals, yet a single male seldom won all encounters with other members of the mating troop. No adult male participated in every bout, and males attracted to a core area of an estrous female included local males as well as some which traveled considerable distances to the site (>200 m in some summer bouts).

Chases were the primary means by which spacing mechanisms were maintained. Number of chases varied with season, sex, and age (Table 2). Three-fourths of the total chases ($N = 555$) occurred during the breeding season, and rate of

Table 2. Chases involving chipmunks of different age and/or sex class during breeding and nonbreeding seasons expressed as a percent of total ($N = 555$)

Participants (Winner/Loser)	Season			Total
	Breeding	Nonbreeding		
		Spring	Autumn	
Adult male/adult male	45.9	0.2	0.5	46.6
Adult male/adult female	19.2	0.0	0.7	19.9
Adult female/adult male	8.1	1.1	4.9	14.1
Adult female/adult female	0.0	1.3	1.8	3.1
Adult male/subadult	0.9	1.4	2.0	4.3
Adult female/subadult	0.0	1.8	2.3	4.1
Adult male/juvenile	0.0	0.4	1.4	1.8
Adult female/juvenile	0.0	0.9	4.0	4.9
Subadult/juvenile	0.0	0.5	0.0	0.5
Juvenile/juvenile	0.0	0.0	0.7	0.7
Total	74.1	7.6	18.3	
Rate of chases[a]	0.98	0.04	0.10	

[a] Rate = number of chases per hour based on 2500 h of field study

chases per h during the breeding season was greater than rate in spring or in autumn. Sixty-two percent of the chases during the breeding season involved pairs of adult males; 37% occurred among adult males and estrous females during mating bouts. Of the total chases, 84% included two adult participants, 15% occurred between an adult and a young animal, and only 1% involved two young animals.

Wolfe (1966) concluded that dominance is directly correlated with body size among chipmunks housed in large outdoor pens. I analyzed chases among adults by comparing body weights and distances to burrow systems of participants to three variables: sex, season, and outcome of chase (winning or losing). Two 3-way analyses of variance were used for these comparisons. Differences in body weight between opponents were significant only when the three variables were considered concurrently ($F = 1308.8$, $P < 0.001$). Weights of adult females involved in a chase were not different with season regardless of whether they won or lost the chase (Student-Newman-Keuls test, $P > 0.05$). This was also true for adult males in spring and autumn, although in the breeding season male winners were larger ($\bar{X} = 105$ g) than losers ($\bar{X} = 102$ g, $P < 0.05$).

Distance of chase from home sites of participants differed with sex ($F = 20.1$, $P < 0.01$) but not with season. Adult males were involved in chases farther from burrow systems ($\bar{X} = 49.3$ m) than were adult females ($\bar{X} = 16.4$ m). Distance also varied when the three factors were considered simultaneously ($F = 116.5$, $P < 0.001$). Males were more likely to win a chase in the breeding season when they were closer to their home sites ($\bar{X} = 48.8$ m) than were opponents to their home sites ($\bar{X} = 51.6$ m, $P < 0.05$). In the nonbreeding season, male and female winners were closer to respective home sites ($\bar{X}$'s $= 9.0 - 11.4$ m) than losers ($\bar{X}$'s $= 17.7 - 41.4$ m, $P < 0.05$); thus, adults within their core areas were dominant and effectively excluded conspecifics. However, adult males in autumn often won encounters which occurred relatively far from their burrow systems ($\bar{X} = 28.3$ m) and core areas. These are examples of defense of individual distance in adult males at autumn sources of mast.

Olfactory and auditory communication are other plausible ways by which spacing can be maintained in mammals. Scent-marking was never observed. I noted nearly 1500 records of vocalizations; 12% were a vocalization termed chipping (see Dunford, 1970) and 92% of these were in response to my presence. Chipping was given only on one occasion by a chipmunk when a conspecific was nearby (<10 m), and this instance occurred during a mating bout. Vocalizations, including chips and chip-trills (terminology after Dunford, 1970), were delivered in 7% of the total chases, but these were emitted by the animal being chased and not by the aggressor.

4. *Mating System*

Estrus occurred twice in the population during each annual cycle. Eight mating bouts were observed during the winter breeding season with the earliest bout recorded on 14 February and the latest on 4 March; 13 bouts were noted in the summer breeding season between 7 and 29 July. Several bouts involving resident, estrous females were not observed, but estimated dates of mating concurred with dates of recorded bouts. Subadult males never displayed breeding behavior. Two subadult females bred but both litters were lost prior to weaning.

Social structure during the breeding season was similar to that in the nonbreeding season, but it changed dramatically on days of estrus. Adult males routinely inspected core areas and entrances of burrow systems used by chipmunks of either sex and investigated all conspecifics encountered during movements each day beginning shortly after sunrise. Several males often congregated for short time periods each morning at a female's core area beginning 2 to 3 days before she emerged to mate. Adult males frequently maintained individual distances when they encountered other adult males during these morning movements or when congregating at core areas of estrous females. On the other hand, territoriality was seldom observed in adult males during the breeding season because little time was spent near their home sites.

Adult females were rarely active above ground in the morning during the breeding season. They restricted activity to afternoon or evening, perhaps in response to morning movements and harassment by adult males. However, an estrous female became active on the morning of the day of peak estrus. I was unable to determine if a female voluntarily emerged from her burrow system prior to males gathering in her core area or whether males actually entered the burrow and evicted her. Once the receptive female emerged, a mating bout ensued and the number of males in the core area of the estrous female increased as the morning progressed. Generally, the number of male participants was higher in summer bouts (2–8) than in winter bouts (1–4);

more males participated in bouts occurring in central portions of the study area than in bouts in remote sectors. The bout sometimes continued until mid-afternoon but often terminated by late morning when the female returned to her burrow system.

Adult males were aggressive throughout a bout, whereas an estrous female initially chased males but retreated from their approach more readily as the bout persisted. When adult males chased the female, high-pitched squeals were given by both sexes as males tried to mount. The female thwarted the advances of males by fleeing of seeking refuge under obstacles or in underground crevices. Brief pairing (after Eisenberg, 1966) and copulation occurred when a single male found the female at the refugium or when a male isolated the female from the rest of the troop for several minutes. When the number of adult male participants in the mating troop was low (2–3), only the dominant male copulated with the estrous female. Because of few troop members, a dominant male easily prevented other males from approaching the estrous female and copulating. On two occasions the troop numbered seven and eight males, respectively, and the dominant male in the troop never copulated because he spent so much time chasing male rivals away from the female. As a result of continual involvement of the dominant male in aggressive interactions, another male was eventually able to chase the estrous female to another area and copulate with her. The dominant male often remained at the same site and continued to chase intruding males even though the female had left the area. Other males continued to be attracted to this site for several hours after the mating bout. Apparently, the female deposited an olfactory cue, perhaps a vaginal or anal secretion.

Smith and Smith (1975) and Elliot (in press) briefly describe copulation as a series of intermittent pelvic thrusts by the mounted male lasting several minutes. I observed copulation in its entirety on nine occasions. Prior to copulation, the female remained stationary within a few centimeters of the lone male. She eventually allowed the male to approach and nudge her flank, rump, or nose. A fight, accompanied by high-pitched squeals, usually preceded mounting and copulation. Then the male mounted the female for approximately 1.5 min ($\bar{X} = 88$ s), clasped her sides with his forelegs, and alternated bursts of pelvic thrusts ($\bar{X} = 7$ s) with nonthrusting periods ($\bar{X} = 8$ s) while occasionally biting her neck region. In some cases, copulation was terminated by the approach of other males. After copulation and dismounting, the male remained near the female unless disturbed by other males, and both simultaneously groomed for several seconds. After grooming, the male usually attempted to mount again but the female often ran from the site.

Copulation occurred on logs and tree stumps, in open areas on the ground, or beneath objects. Copulation probably takes place underground as well because males often followed the female into woodchuck (*Marmota monax*) burrows, vacant chipmunk burrows, or underground crevices created by exposed tree roots along eroded stream banks, and remained there with the female for several minutes. The male emerged from this site only to chase intruding males. I saw as many as four different males copulating with the same female at least once during a single mating bout for a total of seven copulations. A similar mating system is recently reported in a New York population of *Tamias* (Elliot, in press).

5. Mother-Young Association

The number of juveniles weaned per litter, based on 44 litters, ranged from one to four ($\bar{X} = 1.8$). Juveniles initially emerged from the natal burrow system at 45 to 52 days ($\bar{X} = 49$) after birth. Adult females ceased lactating and took small bits of solid food into the system several days prior to emergence of the juveniles. After emergence, juveniles readily investigated and consumed food items found in the vicinity of the system.

A mother chipmunk seldom associated or interacted with her litter above ground. Juveniles directed play behavior toward her, but she always ignored these attempts. Play, however, did occur among littermates prior to their dispersal.

Daily activity of juveniles was confined to areas near the natal system before dispersing. They frequently spent the night alone or as a group in an abandoned system or in any underground cavity in the vicinity of the natal site. Juveniles dispersed from the mother's core area within 3 days of initial emergence, but two litters remained as a unit for 9 and 27 days, respectively. Mother chipmunks were never observed to expel their litters from the core area with aggressive acts, rather, dispersal appeared to occur voluntarily. Juveniles returning to natal core areas several days after dispersal were attacked and chased by their mothers. On two occasions a juvenile did not leave the core area of birth. In one instance the mother disappeared from the study area, and in another the mother moved to a new burrow system located 35 m from the natal system immediately after litter emergence.

Table 3. Duration and frequency of behavioral categories in chipmunk. Each category is expressed both as a percent total time (s) and as a percent total frequency of occurrence (number of times performed) per minute of above-ground activity relative to other categories based on 1279 observation bouts

Behavioral category	Duration	Frequency
Pause	42.61	37.04
Forage	18.76	18.49
Locomotion	16.74	28.07
Eat	11.43	2.79
Groom	2.70	4.08
Scratch	0.56	2.45
Vertical pause	0.51	0.31
Run	0.08	0.22
Climb	0.03	0.03
Drink	0.16	0.40
Collect leaf	0.31	0.31
Collect food	0.38	0.41
Scatter hoard	0.07	0.05
Locomotion-sniff	0.92	0.38
Play	0.06	0.04
Agonistic behavior[a]	2.34	2.47
Threat	(1.22)	(0.69)
Chasing	(0.53)	(0.90)
Being chased	(0.44)	(0.70)
Withdraw	(0.11)	(0.10)
Fight	(0.04)	(0.08)

[a] Includes Threat, Chasing, Being Chased, Withdraw, and Fight

6. *Time Budgets*

Pause occurred more frequently than any other behavioral category and comprised nearly one-half of the population activity above ground (Table 3). This category, combined with forage, eat, and locomotion composed almost 90% of both total duration and frequency of the time budget. In contrast, less than 3% of the total time budget involved agonistic behavior.

Time budgets varied with sex and age class, temporal, spatial, and social factors (Tables 4 and 5). Multivariate F-ratios were significant for single factors (main effects) and for several combination of factors considered simultaneously. For example, time budgets varied with sex class (multivariate F-ratio significant at $P < 0.001$ for both duration and frequency). Differential budgets between males and females resulted from significant variations in duration of groom, threat, chasing, forage, locomotion, eat, agonistic behavior, and locomotion-sniff (Table 4), and in frequency of locomotion, threat, eat, agonistic behavior, play, forage, and locomotion-sniff (Table 5, univariate F-ratios significant at $P < 0.05$ to 0.001). Effects of the remaining five factors or combinations of the six factors can likewise be interpreted.

7. *Individual Behavioral Categories*

Mean duration and frequency of individual behavioral categories which discriminated among levels of a single factor of combination of a particular set of factors and which gave the best biological interpretation of these factors on time budgets were tested for significance among levels. Some of these are presented (Table 6) and discussed below. A more detailed presentation of the analysis of individual behavioral categories is given by Yahner (1977b).

A. Pause. Frequency declined when a chipmunk was within 10 m of another chipmunk, hereafter referred to as conspecific present versus absent (>10 m), compared to the reverse situation. Frequency within the core area was lower than outside the core area, but the reverse was true of duration.

Duration and frequency differed with annual periods. Both were greater in autumn than in spring or in the breeding season. Differential duration with season was in part due to sex class. Males in autumn spent more time at pause ($\bar{X} = 31.5$/min) than at other annual periods or more than females in any season ($\bar{X}$'s ≤ 26.4/min, $P < 0.05$).

B. Forage. This behavior varied among chipmunks of different sex or age class. Duration and frequency of forage in females were greater than in males. Durations in juveniles and subadults were similar but both differed from duration in adults. However, juveniles foraged more frequently than either subadults or adults. Further, adult males spent less time foraging ($\bar{X} = 7.9$/min) than other age-sex classes (X's ≥ 13.0/min, $P < 0.05$).

Table 4. Multivariate analysis of variance of sex-class, age-class, spatial, social, and temporal factors versus durations of 21 behavioral categories

Factor[a]	Multi-variate[b] F-ratio	Significance level of univariate F-ratio[c]		
		$P<0.05$	$P<0.01$	$P<0.001$
Main effects:				
Sex	4.8***	G, T, CG		F, L, E, AG, LSN
Age(2)	4.6***	CF	F, AG, T, CG, PL	L
Age(3)	5.2***	E, CB	G, LSN	F, L, PL, AG, T, CG
Spatial	21.7***		G, CL	P, F, L, E, LSN, AG, T, CG, CD, FT
Social	37.6***	PL		F, E, V, LSN, AG, T, CG, CD, W, FT
Daily	1.8**		F, L	
Season	20.6***		G, B	P, F, L, E, CF, LSN, AG, T, CG, CD, FT
First-order effects:				
Sex × age(3)	1.7*	CL, CB, LSN	F, L	
Sex × spatial	3.1***	AG	L, E, LSN, T, CG	
Sex × social	3.7***	P, CD	V, T	LSN, AG, CG
Sex × season	3.0***	T, CD, FT	G	P, F, L, LSN
Age(2) × season	2.3***	P, E, G	AG	F, L, R
Age(3) × spatial	1.9***	E		F, L
Age(3) × social	5.4***		FT	LSN, AG, T, CG
Spatial × social	4.2***	L, AG	FT	V, LSN, CD
Second-order effects:				
Sex × age(2) × season	1.5*	F, L, CL	R	
Sex × age(3) × social	1.5*			LSN, W
Sex × spatial × social	2.4***		AG, CD	T, CG
Age(3) × spatial × social	2.4***	CD		W
Third-order effects:				
Sex × age(3) × spatial × social	1.5*	CG		

[a] Factors: Age(2) = adult and young; Age(3) = adult, subadult, and juvenile; Spatial = spatial factor; Social = social factor (conspecific present or absent); Daily (diurnal period) and Season (annual period) = temporal factors. Non-dignificant effects ($P>0.05$) are omitted from table

[b] Multivariate test of equality of mean vectors. * $P<0.05$, ** $P<0.01$, *** $P<0.001$

[c] Univariate test of dependent variables based on 1279 observation bouts. Dependent variables are durations (s/min) of behavioral categories designated by symbols given in Table 1. Non-significant behavioral categories which do not contribute to the discrimination between effects are omitted from table

Duration was lower in the breeding season than in autumn but was greatest in spring. Frequency also varied among annual periods. Chipmunks foraged for briefer periods when a conspecific was present than when alone; the same trend held for frequency. Duration and frequency were greater within core areas than outside core areas.

Table 5. Multivariate analysis of variance of sex-class, age-class, spatial, social, and temporal factors versus frequencies of 21 behavioral categories

Factor[a]	Multi-variate[b] F-ratio	Significance level of univariate F-ratio[c]		
		$P<0.05$	$P<0.01$	$P<0.001$
Main effects:				
Sex	5.5***	L, T	E. AG	P. F. LSN
Age(2)	3.9***	F, CF. CB. PL. AG	CG	R. T
Age(3)	5.1***	R. E. CF	CB. LSN	F. L. S. R. PL. AG. T. CG
Spatial	14.3***	G	P. CL	F. L. E. LSN. AG, T. CG. CD. FT
Social	47.0***	G. S		P. F. L. E. V, PL, LSN, AG. T, W, CG, CD, FT
Daily	1.7**	CF, CB	L	
Season	13.0***		B	P, F. L, E. G, CF, LSN, AG. T, CG, CD, FT,
First-order effects:				
Sex × age(3)	1.9***	L, D, CL, LSN	CB	PL
Sex × spatial	2.6***	R, CF, AG	T	F, LSN, CG
Sex × social	4.2***	E, T	AG, W	PL, LSN
Sex × season	2.1***	F, CD		S, LSN
Age(2) × season	1.8**	E, LSN	R, AG	
Age(3) × spatial	2.2***	LSN		F
Age(3) × social	6.1***		V	PL, LSN, AG, T, CG, W, FT
Spatial × social	6.1***	AG	L	V, PL. LSN, CD, FT
Daily × season	1.6***		AG	P, CB
Second-order effects:				
Sex × age(3) social	2.5***		LSN	PL. W
Sex × spatial × social	2.6***	P, PL, LSN, AG	CD	T, CG
Sex × daily × season	1.5**	S		CB. CD
Age(3) × spatial × social	3.6***	CD		V, PL, W
Age(2) × daily × season	1.3*			R, CB
Third-order effects:				
Sex × age(3) × spatial × social	2.4***		AG. T. CG	PL

[a] Factors: Age(2) = adult and young; Age(3) = adult, subadult, and juvenile; Spatial = spatial factor; Social = social factor (conspecific present or absent); Daily (diurnal period) and Season (annual period) = temporal factors. Non-significant effects ($P>0.05$) are omitted from table

[b] Multivariate test of equality of mean vectors. * $P<0.05$. ** $P<0.01$, *** $P<0.001$

[c] Univariate test of dependent variables based on 1279 observation bouts. Dependent variables are frequencies (actual number of times performed/min) of behavioral categories designated by symbols given in Table 1. Nonsignificant behavioral categories which do not contribute to the discrimination between effects are omitted from table

Table 6. Mean duration and frequency of selected behavioral categories among levels of sex, age, spatial, social and seasonal factors

Behavioral category	Sex class		Age class[a]			Spatial[b]		Social[c]		Season[d]		
	Male	Female	A	S	J	In	Out	ABS	PRES	BR	SP	AU
D-Pause[e]						27.2	24.0***			24.1	23.5	28.4*
F-Pause						4.2	4.7***	4.6	3.4***	4.0	4.0	5.0*
D-Forage	10.0	13.3***	10.2	13.4	15.4*	12.9	8.9***	12.6	6.6***	6.7	19.8	9.8*
F-Forage	1.7	2.7***	2.0	2.2	3.0*	2.3	1.9***	2.4	1.1***	1.2	2.8	2.4*
D-Locomotion	12.5	7.7**	11.9	6.7	6.9*					17.6	6.7	8.5*
F-Locomotion	3.4	3.3*	3.4	2.7	3.7*							
D-Eat	5.3	9.1***	6.4	8.9	7.8*	8.3	4.7***	7.8	3.7***	2.6	7.0	9.0*
F-Eat	0.3	0.4**	0.3	0.4	0.3*	0.4	0.3***	0.4	0.2***	0.2	0.5	0.3*
D-Groom			1.8	1.8	1.0*	1.9	1.2**					
F-Groom						0.5	0.4*					
D-Collect food										0.00	0.005	0.45*
F-Collect food										0.00	0.001	0.09*
D-Play			0.00	0.00	0.04*							
F-Play			0.00	0.00	0.03*							
D-Threat	1.03	0.43*	1.07	0.05	0.15*	0.44	1.34***			1.99	0.39	0.25*
F-Threat	0.11	0.05*	0.12	0.01	0.01*	0.05	0.14***			0.19	0.03	0.01*
D-Chasing	0.46	0.18***	0.19	0.01	0.01*	0.19	0.59***			0.88	0.25	0.12*
F-Chasing			0.16	0.01	0.01*	0.06	0.20***			0.28	0.05	0.03*
D-Being chased						0.14	0.53*					
F-Being chased						0.04	0.18*					
D-Withdraw	0.004	0.502*										
F-Withdraw			0.04	0.14	0.11*							
D-Fight			0.17	0.01	0.00*	0.01	0.05*			0.081	0.006	0.004*
F-Fight			0.07	0.01	0.00*	0.003	0.022*			0.033	0.003	0.002*

[a] A = adult; S = subadult; J = juvenile

[b] Spatial = spatial factor; where In = within core area, Out = outside core area

[c] Social = social factor; where ABS = conspecific absent, PRES = conspecific present

[d] BR = breeding season; SP = spring; AU = autumn

[e] D = duration (s/min); F = frequency (number of times performed/min). * $P<0.05$, ** $P<0.01$, *** $P<0.001$ based on univariate F-ratios taken from Tables 4 and 5 when the number of levels within a factor consisted of two or on the level of significance obtained a posteriori by the Student-Newman-Keuls test (Sokal and Rohlf, 1969) when levels exceeded two

C. Locomotion. Male chipmunks were more mobile than females. Duration and frequency in males differed from duration and frequency in females. In general, time budgets of adults included a higher proportion of locomotory behavior than those of younger individuals. Duration in adults was significantly greater than durations in either subadults or juveniles. However, frequencies in adults and in juveniles were equal, but both exceeded frequency in adults.

Duration during the breeding season was greater than in autumn yet lower in spring than in other annual periods. To illustrate the fact that adult males were exceedingly conspicuous in the breeding season because of extensive, wide-ranging movements and that they also spent considerable time outside their core areas in autumn. duration in adult males was similar in the breeding season ($\bar{X} = 12.8$/min) and in autmn ($\bar{X} = 11.1$/min). However, these durations were greater than both adult males in spring or any other age-sex class during all annual periods ($\bar{X} = 5.92$–9.98/min, $P < 0.05$).

D. Eat. Females spent more time eating than males; frequency varied similarly. Duration in subadults exceeded duration in adults, but neither of these differed significantly from duration in juveniles. Frequency likewise varied between adults and subadults but not from juveniles.

Duration in spring was higher than that in the breeding season but less than duration in autumn. Frequency was lower in the breeding season than at other annual periods. However, unlike duration, frequency in spring exceeded that of autumn.

The presence versus absence of a conspecific resulted in a marked difference in duration and frequency of eat. More time was allocated to eating within core areas than outside core areas, and this behavioral category occurred more often near home sites.

E. Groom. Durations did not differ among adults and subadults but were greater than juveniles. Chipmunks spent more time grooming within their core areas than outside these areas. Similarly, frequency declined outside core areas.

F. Collect Food. Duration was greater in adults ($\bar{X} = 0.28$/min) than in young ($\bar{X} = 0.12$/min, $P < 0.05$); frequency likewise varied with age ($\bar{X} = 0.05$ versus 0.03 per min, $P < 0.05$). I did not observe collect food in the breeding season. Duration and frequency during autumn were much higher than spring.

G. Play. Only juveniles exhibited play. Play was observed prior to dispersal near entrances to natal burrow systems. Solitary play (Ferron, 1975) was not recorded.

H. Threat. Duration and frequency in males were greater than duration and frequency in females. Durations in juveniles and subadults were similar but both were lower than duration in adults; this trend held for frequencies as well.

Duration and frequency outside core areas exceeded those within core areas. Duration and frequency during the breeding season were higher than duration and frequency during spring and autumn. Differential duration with season was mainly due to sex class. Males in the breeding season spent more time at threat ($\bar{X} = 2.2$/min) than females or males at other annual periods ($\bar{X} = 0.3$–0.7/min, $P < 0.05$).

I. Chasing. Duration differed with sex class. Duration and frequency in adults were greater than either subadults of juveniles.

Duration and frequency within core areas were less than those outside core areas. The effect of home site location on chasing was best interpreted when sex class was also considered. Duration was greater in males outside their core areas ($\bar{X} = 0.79$/min) compared to males within core areas or females regardless of home site location ($\bar{X}$'s $\leqq 0.16$/min, $P < 0.05$). The same pattern followed for frequency ($\bar{X} = 0.26$/min versus $\bar{X} = 0.03$–0.08/min, $P < 0.05$). Duration and frequency during the breeding season exceeded durations and frequencies in spring and in autumn.

J. Being Chased. Duration and frequency outside core areas were greater than when chipmunks were within their core areas. As with chasing, duration and frequency of being chased varied with season and sex class. Duration ($\bar{X} = 1.30$/min) and frequency ($\bar{X} = 0.34$/min) of females during the breeding season exceeded males ($\bar{X} = 0.72$/min and 0.20/min, $P < 0.05$), but these were higher than durations ($\bar{X} = 0.05$–0.20/min, $P < 0.05$) and frequencies ($\bar{X} = 0.01$–0.07/min, $P < 0.05$) of the remaining sex-annual period combinations. Frequency was greater in females during morning in the breeding season ($\bar{X} = 1.00$/min) than at other times of the day or year or compared to males regardless of annual-diurnal period ($\bar{X}$'s $\leqq 0.32$/min, $P < 0.05$). This attests to the continuous harassment of estrous females by adult males during the mating bouts.

K. Withdraw. Duration was greater in females than in males. Frequencies in juveniles and in subadults were similar but both exceeded frequency in adults.

L. Fight. Duration and frequency in the breeding season were greater than spring or autumn. In the breeding season, duration in females ($\bar{X} = 0.16$/min) was higher than duration in males ($\bar{X} = 0.07$/min, $P < 0.05$). In summary, agonistic encounters were very intense during mating bouts, and fighting was more likely to occur between an estrous female and an adult male or between two rival males participating in a bout than at other times of the year.

Fights consumed more time outside core areas than within. Frequency likewise was higher away from home sites. Juveniles were never observed to fight; duration and frequency in subadults were less than those in adults.

8. *Individual Social Response to Conspecifics*

The rotated factor matrix of 25 chipmunks represented in one or more age classes was composed of four factors accounting for 96.5% of the total variation (Table 7). Factor I is an 'attentive' factor because animals in this group spend considerable time at pause, i.e., fixating on a conspecific, when a conspecific is in

Table 7. Oblimin rotated factor matrix of the behavior of 25 chipmunks represented as adults, subadults, and juveniles

Variable[a]	ID[b]	Sex[c]	Age[d]	I[e]	II	III	IV
1	79	F	A		0.52	0.45	
2	81	F	A	0.86			
3	117	M	A	0.93			
4	128	M	A		0.58	0.61	
5	137	F	A	0.97			
6	170	F	A	0.62			
7	175	M	A	0.77			
8	179	F	A	0.78			
9	186	M	A		1.00		
10	258	F	A		0.96		
11	431	M	J				0.94
12	431		S				0.59
13	431		A	0.45		0.71	
14	456	F	A	0.72			
15	463	M	A	0.99			
16	465	F	S		0.52		
17	465		A	0.88			
18	505	F	S	0.98			
19	515	M	J	0.48	0.63		
20	515		S	0.95			
21	534	F	J	0.68			0.59
22	546	F	J	0.91			
23	565	F	J	1.04			
24	565		S	0.49	0.72		
25	607	M	J	0.70	0.46		
26	607		S	0.99			
27	612	F	A	0.78			
28	651	F	J	0.71	0.51		
29	664	M	S	0.74			
30	675	M	J	1.07			
31	676	F	J	0.99			
% Variation explained				75.7	11.4	5.6	3.8

[a] Variables represent chipmunks of a specific age class

[b] Number of ear tag identifying each individual

[c] *M* = male; *F* = female

[d] *A* = adult; *S* = subadult; *J* = juvenile

[e] Factors extracted from Q-factor analysis; cases = mean durations and frequencies of 20 behavioral categories recorded in observation bouts during the nonbreeding season when in the presence of a conspecific; 0.45 factor loading throughout

the vicinity. This factor explains 75.7% of the total variation. Factor II is an axis containing chipmunks which forage a great deal despite the presence of another chipmunk and is termed 'foraging' accounting for 11.4% of the total variation. Factor III is designated a 'locomotion-aggressive' factor. Animals with high loadings for this factor move about extensively and frequently respond to a nearby conspecific with threats and chases. This factor explains 5.6% of the total variation. Factor IV is 'eating' and represents chipmunks who spend appreci-

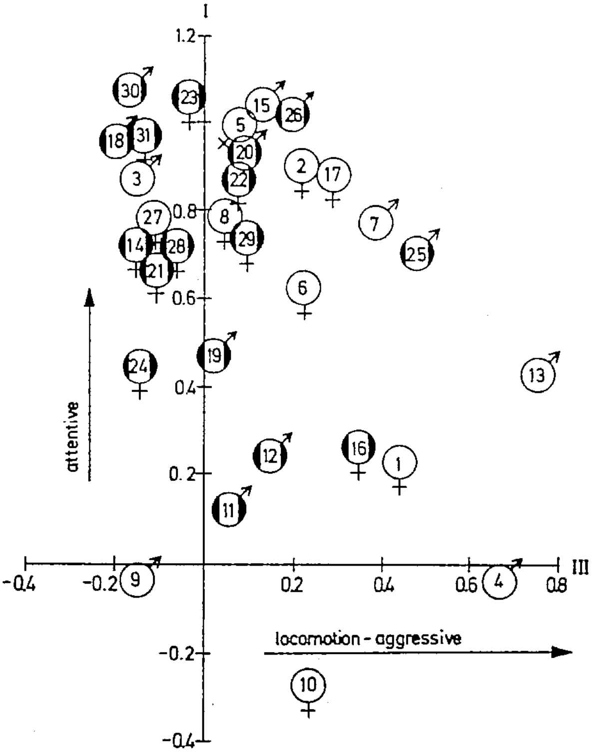

Fig. 2. Plot of 'locomotion-aggressive' factor, III, on 'aggressive' factor, I, extracted by Q-factor analysis. *Open circles* = adults; *shaded circles* = young (juveniles or subadults). Enclosed numbers correspond to variable numbers of individuals as given in Table 7

able time eating even though another chipmunk is present. This factor accounts for the remaining 3.8% of the total explained variation.

A plot of Factor III on Factor I (Fig. 2) gives the best visual and biologically interpretable illustration of the data. A majority of the chipmunks lie along the upper portion of the y-axis (Factor I) with variable degrees of individual 'attentiveness' in the presence of a conspecific. Chipmunks positioned near the intercept of the x- and y-axis eat or forage in the presence of a conspecific. The position of individuals relative to the y-axis may be taken as a measure of aggression. Eight (47%) of the young (subadults and juveniles) and only three (21%) of the adults are to the left of this axis. These individuals avoided agonistic encounters and were considered unaggressive. In contrast, 11 (79%) of the adults and only nine (53%) of the young are found to the right of the y-axis. These animals were involved in more agonistic encounters than the unaggresive individuals and were intolerant of nearby conspecifics.

Based on data available for a few individuals represented in more than one age class, behavioral profiles may change with age. The level of aggresiveness in male 515 remained relatively unchanged as a juvenile and a subadult, but the level of its attentiveness increased with age (see variables #19 and 20 in Table 7 and Fig. 2). Similarly, female 465 increased attentiveness as she became older (#16 and 17). Male 431 spent considerable time eating both as a juvenile (#11) and a subadult (#12) despite the presence of a nearby conspecific but increased its level of aggresiveness as an adult (#13).

Behavioral profiles of adults (Fig. 2), based on factors I and III, coincided with differences in reproductive fitness. Adult females to the right of the y-axis successfully mated and reared litters. The adult female to the left of the axis never came into estrus. Adult males to the left of the axis (unaggressive males) participated in mating bouts but never copulated with an estrous female because other males in the mating troop always dominated and prevented them from approaching and mating with her. These three unaggressive adults were tolerant of conspecifics during the nonbreeding season and seldom or never exhibited territorial defense of their core area, whereas the adults located to the right of the y-axis always excluded trespassers from their core areas. Thus, increased reproductive fitness appears to be associated with territoriality in eastern chipmunks.

Discussion

1. Social Organization and Spacing Mechanisms

The social system of the chipmunk population in this study typified that of a mammalian species adapted to a solitary and dispersed way of life. The rearing strategy of *Tamias*, an important component of the social system, is indicative of this and can be interpreted from an evolutionary perspective. Firstly, the extended period of development within a secure, underground nest subsequent to a lengthy gestation period permit juveniles to attain appreciable size prior to emergence (Yahner, 1978a). Secondly, juveniles possibly learn relevant food types from the mother prior to surface activity and do not have to spend considerable time after emergence searching for an learning appropriate food types, thereby decreasing foraging movements and predation risks. The adaptiveness of this strategy is that it maximizes a female's reproductive fitness because juveniles are self-reliant once emergence occurs. Thus, selection has favored reduced fecundity per litter, long postnatal development, and early dispersal which permits bi-annual breeding in southern populations (Yahner and Svendsen, 1978)—a phenomenon which seldom exists in other species of hibernating ground squirrels.

Chipmunks apparently find adequate food near home sites because foraging and eating activities are centered in core areas surrounding burrow systems (Tables 4–6). Permanent social units beyond that of the individual are therefore not adaptive in *Tamias* because group formation requires a large home range and greater foraging movements to obtain adequate resources (after Eisenberg, 1966; Smith, 1968; Crook et al., 1976). Perhaps these constraints on group size explain why effective dispersal mechansims have evolved and few juveniles remain near birth sites after dispersal (Fig. 1).

Although eastern chipmunks are solitary during the entire annual cycle, the timing of mating is remarkably synchronized by sex-specific mating behavior. Adult males, which are normally sedentary and inconspicuous during the nonbreeding season, become highly mobile during the breeding season (Tables 4 and 5) increasing their chances of locating core areas inhabited by estrous females. Then, by visiting these sites each morning, adult males are likely to be in the locality on the morning in which the female emerges to mate. Interestingly, movements in adult males in the winter breeding season are generally less extensive compared to those in the summer breeding season (usually <50 m in the winter versus >200 m on occasion in the summer). Perhaps reduced movements in the winter breeding season result from physiological intolerance of low ambient temperatures for extended periods thereby limiting distances traveled and time spent searching for estrous females. Reduced movements may also be adaptive in the winter breeding season because of increased predation risks. During February and early March no herbaceous growth or canopy cover is present, which likely increases a predator's chances of detecting a wandering chipmunk.

Adult females, on the other hand, typically confine most movements to their core areas regardless of season (Yahner, in press). During estrus, which may last 3 to 10 days (Smith and Smith, 1975), a female presumably attracts wandering adult males to her core area by olfactory mechanisms (see Dobroruka, 1972). Evidence for some sort of olfactory cue is based on observations of behavior and extended activity of adult males in a core area of a specific female beginning several days prior to a mating bout involving that female. By 'advertising' her reproductive status well in advance of the date of mating, a female increases the likelihood that adult males find her and copulate with her when she is receptive. Further, successful copulation is insured on the day of mating because the estrous female relaxes defense of her core area and mates with several males during a single bout. A similar mating system has evolved in other solitary, forest-dwelling sciurids (Smith, 1968; Farentinos, 1974; Elliot, in press).

The three spacing mechanisms determining the social system during the annual cycle—defense of individual distance, relative dominance hierarchies, and territoriality—are effective adaptations to augment exploitation of resources so that maximum survival and reproductive fitness may be ensured. Defense of individual distance is a rudimentary spacing mechanism (Stokes and Cox, 1970) and involves defense of a personal sphere against conspecifics without regard to a fixed site (Brown, 1975). Defense of individual distance was common during autumn when chipmunks move outside core areas to harvest mast or during the breeding season when adult males encountered one another in their search for estrous females. Infrequent chases by subadults and juveniles (Table 2) were probable examples of this. Young animals rarely fought, threatened, or chased conspecifics (Tables 4 and 5), and the ontogeny of territorial and reproductive behavior coincided with increased levels of agressiveness as chipmunks attained adult status. Threatening may be a means of increasing an animal's readiness to act aggressively and could result partially from a learning process through a series of aggressive encounters (Barnett and Evans, 1965). Thus, I suggest that intermittent exposure of young to agonistic situations with aggressive, territorial adults may provide experience in developing appropriate responses toward other chipmunks. The adaptive consequence of the ontogeny of aggressive behavior not only insures effective defense of home sites, but more importantly from a fitness viewpoint, it allows an individual to compete successfully for potential mates when adulthood is reached (Table 7 and Fig. 2). The ontogeny of aggressive behavior is exemplified in male 431. As a juvenile and a subadult, 431 seldom exhibited aggressiveness toward conspecifics; but he began to defend his core area from others at about 10 month of age. Then as an adult, 431 copulated with every estrous female in mating bouts in which I observed his participation.

Dominance hierarchies were formed among adult males during mating bouts. Individual recognition was improbable because male composition of mating troops varied among bouts and some males traveled to sites of mating bouts which were never traversed by these individuals at other times of the year. This, combined with the high rates of aggressive encounters among members of the mating troop (Table 2), implies that the hierarchy formed was relative, rather than absolute, because an absolute hierarchy requires individual recognition and acts to reduce conflict (after Etkin, 1971).

The third spacing mechanism, territoriality, was observed throughout the year in adults. A regular dispersion of burrow systems was at least partially due to defense of core areas. Territorial behavior in *Tamias* is a consequence of several proximate factors including food resources and habitat characteristics. Seasonal food resources of chipmunks are evenly distributed in optimal habitat (Svendsen and Yahner, in press), and in autumn a concentrated cache of mast is hoarded within a *hibernaculum* to sustain underground, nontorpid periods of activity during winter. Mast is only available in quantities for rapid harvest for a few weeks prior to torpor (Yahner, 1975). Therefore, the spacing pattern that results from territorial behavior exhibited throughout the year probably guarantees resident individuals an adequate share of the mast crop. A similar hypothesis is used to explain the adaptive nature of year-round territoriality in other sciurids, such as *Tamiasciurus* spp. (Smith, 1968) and *Eutamias amoenus* (Heller, 1971), which also hoard a seasonal food source. The observation that chipmunks do not permanently inhabit areas devoid of mast-producing trees (Svendsen and Yahner, in press), strengthens the contention that mast supplies are the major resource defended by adult chipmunks.

Species of 'open' grassland (e.g. *Cynomys ludovicianus*; King, 1955) form groups to presumably facilitate predator detection; whereas species such as *Tamias*, occupying a more 'complex' forest environment, tend to remain solitary (after Eisenberg, 1966; Crook et al., 1976). Because chipmunks are diurnal and rely extensively on vision, they prefer areas in the forest which reduce 'noise' in the visual channel. Thus, burrow systems were found at highest densities in habitat offering minimum herbaceous ($\leqq 22\%$ ground cover) and understory growth ($\bar{X} = 1.8$ woody shrubs/m^2) (Svendsen and Yahner, in press). Preference for this type of habitat, together with secretive, inconspicuous movements within core areas during a major portion of the annual cycle, increase the likelihood that a solitary chipmunk can detect nearby predators.

The three spacing mechanisms observed in my population were maintained by aggressive behavior. Aggressive behavior exhibited by territorial adults can ultimately be explained as a behavioral adaptation to aid in competing for resources which maximize survival and reproductive fitness (Fig. 2). Although high levels of aggressiveness enhanced survival by insuring adequate defense of home sites, it also decreased fitness under certain circumstances. For example, dominance was adaptive in adult males when few males were involved in a bout, because the most aggressive male successfully prevented other male rivals from approaching the estrous female to mate. However, if many males participated in a bout, dominance bestowed by extreme aggressiveness inhibited a highly aggressive male from mating because he wasted considerable time and energy defending the female from other males. This often occurred when seven or eight males comprised the mating troop.

Deferred age of sexual maturity and first breeding in young males may be interpreted as an adaptive consequence of intense competition with adult males for females. Young males never won encounters with older and larger animals (Table 2); precocious sexual activity and participation in mating bouts with mature males might significantly increase a young male's chances of early mortality or at least be energetically expensive (see Lill, 1974). Because lactation demands high energy expenditure in rodents (Lynch, 1973), and female chipmunks declined 7 to 10% in body weight during lactation, young females maximize fitness by postponing the date of initial breeding until adequate body size (≥ 85 g) is reached to sustain the cost of raising a litter.

I have no evidence suggesting that auditory or olfactory communication acts to space individuals. Brand (1976) also reported that vocalizations play no role in maintaining spatial distribution in other chipmunks (*Eutamias*). Although ground squirrels (*Spermophilus*) frequently scent mark by rubbing oral and dorsal glands against substrata (Steiner, 1974), development and use of these glands in this genus correlate with complexity of social organization. Solitary species of *Spermophilus* do not mark except perhaps in a passive manner when squirrels accidently touch tunnels of burrow systems while entering or leaving (Kivett et al., 1976), supporting the hypothesis that marking behavior need not be present in a solitary species (Eisenberg and Kleiman, 1972). Mucous and sebaceous glands occur in *Tamias* (Quay, 1965), but dorsal glands are absent (Yahner et al., in prep.). Therefore, olfaction in *Tamias* conceivably functions only indirectly, if at all, in communication during the nonbreeding season.

2. Adaptiveness of Behavior and Its Effect on Social Organization

Chipmunks spent less than one-third of the total annual and diurnal cycles above ground. Behavioral categories comprising the time budget were strongly influenced by proximate factors.

A. Pause. Pause was the most prominent behavioral category in the total time budget (Table 3). Chipmunks continually reconnoitered the environment for potential predators or trespassing conspecifics because predator detection and defense of core areas are the responsibility only of the solitary individual. Other sciurids, such as *S. columbianus*, which inhabit open terrain and form complex social units spend considerably less time at this type of behavior (Betts, 1976).

A chipmunk responded to a nearby conspecific by pausing less often but for longer periods of time because its attention was directed to the approach of the conspecific. Frequency of pause increased when a chipmunk ranged outside the boundaries of its core area and into less familiar sectors of the habitat (Tables 4–6). This was especially true during harvest of mast in autumn which sometimes required long-distant movements (Yahner, 1977b, in press). A mast source was often located in an area never traversed by a particular animal at other times of the year; thus, divergence from a normally sedentary and secretive way of life to one characterized by conspicuous movements into habitat where refugia were not readily known necessitated an increased monitoring of the environment for potential predators to maximize survival.

B. Forage and Eat. Forage and eat constituted a smaller percent of the total time budget (Table 3) than those of social, herbivorous sciurids occupying grassland habitat (e.g. *C. ludovicianus*, King, 1955; *S. columbianus*, Betts, 1976). Smith (1968) and Horn (1968) have shown that the energetics of foraging depend upon the spatial and temporal availability of food resources. Duration and frequency of forage and eat varied relative to the location of home sites and with season (Tables 4–6). After permanent cessation of periods of torpor in late March or April (Fig. 1), food of *Tamias* includes invertebrates, bulbs and seeds of herbaceous plants, and possibly remaining mast stored within the *hibernacula* in the previous autumn (Wrazen, 1976). Because spring food items are found near home sites (Svendsen and Yahner, in press), daily metabolic needs during most of the year were usually met without resorting to wide-ranging foraging movements beyond boundaries of core areas. Energy derived per unit foraging time in spring, however, was presumably low because these items were dispersed and generally small in size; time spent foraging in spring was relatively higher than that allocated to eating (mean forage duration/eat duration = 2.8). Foraging for mast is more profitable in autumn because it is a large food item and is produced in abundant, localized quantities (mean density of mast in the 1.75-ha sector, based on thirteen 1-m^2 quadrats, ranged from 0–18 mast items/m^2 during October). Thus, the Forage/Eat ratio of duration declined in autumn (ratio = 1.1, this represented a 2.5-fold decrease compared to the spring ratio), and more energy was derived with less forage expense.

Duration and frequence of forage and eat in adult females exceeded those in adult males (Tables 4 and 5). Assuming that a female weaned two litters per year (as true of at least 20% of the resident adult females in both 1974 and 1975; Yahner and Svendsen, 1978), 5 to 6 months of the annual cycle would be devoted to parental care of young (gestation and lactation). Thus, increased food intake in adult females would be expected to sustain the metabolic demands of successfully rearing young to maximize reproductive fitness. High duration and frequency of forage and eat in juveniles and subadults (Table 6) may be explained as an adaptation to permit rapid weight gain to insure breeding and territorial defense accrued by attaining adult body size.

C. Locomotion. Chipmunks typically extend activities beyond respective core areas only to harvest mast or to mate. *Tamias* exhibits no major fat accumulation prior to recurrent periods of winter torpor lasting 1 to 6 days (Panuska, 1959) but has evolved a behavioral mechanism of food storage (Brenner, 1975). Transportation of sufficient winter food supplies in autumn to a burrow cache requires a great deal of movement (Tables 4–6). In contrast, locomotion is a minor constituent of the time budgets of colonial sciurids which are classical hibernators and feed continually on succulent vegetation to gain body fat which may serve as an energy source during hibernation (e.g. *M. flaviventris*, Travis and Armitage, 1972).

Locomotion was greatest in morning, particularly during the breeding season (Tables 4 and 5). This was partially due to movements by adult males at these times which conferred selective advantages by increasing their chances of finding and mating with estrous females. In contrast, young chipmunks seldom exhibited breeding behavior, and adult females used olfactory mechanisms within their core areas to solicit mates. Thus, the occurrence and time allocated to locomotion in these age-sex classes were considerably lower than those in adult males.

D. Groom. Self-grooming was observed in chipmunks, but allo-grooming, common to social sciurids (e.g. *Sphermophilus* spp., Steiner, 1973), was absent. Steiner (1973) made a distinction between ordinary and hurried self-grooming in *Spermophilus*. Ordinary grooming was often performed in these sciurids for long periods of time and appeared to be associated with low-key activity. Hurried grooming, however, was suggested to be 'displacement grooming' because it consisted of rapid, jerky motions and was often performed during mating activity. Grooming in *Tamias*, which often occurred on an elevated perch within the core area and was intermingled with scratching and pausing activities (Yahner, 1977b), may be comfort-related and analogous to ordinary grooming in *Spermophilus*. Chipmunks also exhibited ordinary grooming after eating or immediately after emerging above ground at the entrance of burrow systems subsequent to larder hoarding and may have involved the dissemination of scent over the body. A type of grooming similar to Steiner's hurried grooming occurred immediately after copulation and sometimes after chases during mating bouts. These may be examples of displacement or perhaps expressions of dominance after conflict situations (after Armitage, 1976).

E. Hoarding. Chipmunks hoard food throughout the year if localized, abundant food sources exist, as for example, when artificially high concentrations of food are supplied as part of the experimental design in field studies (see Dunford, 1970). However, concentrations of food were seldom found during the year in my study except in autumn when both scatter and larder hoarding occurred. The former was the less frequent behavior, occurred slightly earlier in the annual cycle, and was not exhibited by all individuals. Larder hoarding is the more adaptive method of food storage (Yahner, 1975).

Periods of torpor generally commenced in October and terminated in April (Fig. 1); thus, mast is a vital food source because it must sustain a chipmunk for an approximate 6-month period. With this in mind, mast is understandably an important proximate factor in the evolution of territoriality and caching behavior. What is surprising, however, is the fact that individuals began larder hoarding only 2 weeks or less prior to beginning torpor, although mast was available at an earlier date: yet enough food was stored within the *hibernacula* during this brief time period to provide an adequate resource supply. Although this rapid harvesting of food results in a conspicuous and pronounced increase in activity, predation risks are minimized by restricting hoarding to a brief portion of the annual cycle.

F. Agonistic Behavior. A regular dispersion of burrow systems used by resident chipmunks combined with few movements outside core areas in the nonbreeding season resulted in minimal expenditure of time, and presumably energy, in defense of home sites (Tables 2 and 3). Differences in duration and frequency of agonistic behavior over season are attributed mainly to breeding behavior exhibited by adult males (Tables 4–6). Adult males were involved in most intraspecific encounters (Table 2) due to regular defense of individual distances and establishment of dominance hierarchies during mating bouts. Increased aggression and intense competition among adult males for females during the breeding season are found in many other rodents (Turner and Iverson, 1973; Farentinos, 1974).

G. Play. Play is a common and important behavioral activity in social species and is least likely in small mammals which mature rapidly and disperse at an early age (Ewer, 1968). The lack of mother-young interactions above ground and the brief association of litter mates after emergence reduced opportunities for chipmunks to develop social exchanges. Therefore, minimal play (Table 3), absence of contact-promoting behaviors (such as allo-grooming), and aggressive tendencies toward conspecifics did not promote cohesive social groupings (after Eisenberg, 1967; Skirrow and Rysan, 1976). As a result of these behavioral features, a solitary social structure has evolved in *Tamias* that maximizes survival and reproductive fitness.

3. Population Regulation and Spatual Distribution

At a given season or under a certain set of ecological conditions, the key factor regulating population densities and patterns of dispersion may be food, territorial behavior, or an interaction of several factors (Crook, 1970). Although food supplies partially determined population size and spatial distribution of chipmunks in my study and in other species of chipmunks (*Eutamias;* Brown, 1971; Sheppard, 1971), the evolutionary significance of a characteristic density or dispersion should be explained in ultimate terms (Chitty, 1967).

Territoriality is a mechanism to defend mast, which is a resource in short supply, thereby increasing the probability of individual survival. The regulation of population density is simply the by-product of the mechanism and of the solitary, asocial structure. Territoriality by adults serves to space out individuals into nonoverlapping core areas within suitable habitat offering relatively sparse herbaceous and understory growth and an autumn source of mast. Once home sites are established, chipmunks seldom shift to new areas as adults (Yahner, in press).

The pattern of distribution is usually also the outcome of dispersal tendencies which vary among species, with density and structure of populations, or because of environmental constraints (Brown, 1975). A natural response of a subordinate animal, regardless of species, is to move from a populated area where it is under forced submission to an area from which it is not excluded by dominant individuals (King, 1973). Population density increased appreciably in May and October when juveniles emerged from natal burrow systems and began to disperse (Fig. 1). Because juveniles were seldom aggressive and were subordinate to resident, territorial adults (Tables 2, 4–6), many were forced to disperse to vacant core areas used by previous residents, to suboptimal habitat, or to distant areas. Those juveniles which settled in peripheral, suboptimal areas were likely to be at a disadvantage compared to those which settled in vacant, optimal habitat. Peripheral areas were characterized by dense vegetation and usually lacked in proximal source of mast.

A question asked in this study is whether or not the population is self-regulated. Self-regulatory mechanisms (intrinsic mechanisms) may take the form of cannibalism, reduced gonadal growth, interruption of gestation or maternal care, or dispersal resulting from aggressive behavior (see Slade and Balph, 1974, for review). Extrinsic factors may include predation, weather, starvation, or disease, which include both density-dependent and density-independent processes (Krebs, 1973). Evidence suggests that populations of ground squirrels (*Spermophilus* spp.) are not regulated solely by either intrinsic or extrinsic processes, but rather by a complex interaction of several factors (Carl, 1971; Slade and Balph, 1974). Such is the case with my population of chipmunks. Because dispersal was, at least partially, the response of subordinate juveniles to social pressures exerted on them by dominant resident animals, the present population may be considered self-regulatory. Dispersal typically involved extensive movements; therefore, predation (an extrinsic factor) may have removed a significant proportion of those individuals moving from their place of birth in May and October to establish new home sites. Several chipmunks disappeared each year from the study area in the time period between the onset and cessation of winter torpor (Fig. 1), suggesting that these possible deaths were due to natural causes within *hibernacula*, weather factors, or failure of some animals to store ample food in autumn to survive periods of nontorpidity during the winter months. Annual percentage of winter mortality reportedly varies as much as 44 (Yerger, 1955) to 90% (Linduska, 1949) in other studies of chipmunk populations.

4. Concluding Remarks

The social system and behavior of chipmunks on my study area represent a compromise among various selective pressures which maximize individual survival and reproductive fitness. Behavior is a major determinant of the social system, and both are influenced by demographic, temporal, spatial, and social factors. Population dynamics and spatial distribution of chipmunk populations are partially the result of the social system and behavior. An analysis of each component of the social system and a quantitative approach to the study of behavior is an important step to develop a comprehensive model of the sociobiology of different sciurid species exploiting a variety of environmental types.

Acknowledgements. I thank Gerald E. Svendsen for many discussions on several aspects of this study and for his critical review of this manuscript. I am also grateful to William D. Hummon, Jerome S. Rovner, Henri C. Seibert, James A. Wilson, and Warren A. Wistendahl for their helpful comments and careful evaluation of the manuscript. I thank Barbara B. Beach and Marleigh T. Hartman for preparing the manuscript. I especially extend warmest appreciation to my wife, Darlinda, and to my parents for their endless encouragement and assistance during all phases of this research project. Funds for this study were provided by the Department of Zoology and Microbiology at Ohio University a Grant-in-Aid of Research from Sigma Xi, and an Ohio Biological Survey Grant (UT 1673) to G.E. Svendsen. I dedicate this paper to my dearest friend, my father, who passed away at the termination of this study.

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