Response of the eastern chipmunk, *Tamias striatus*, to sex ratio manipulations

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We hypothesize that male and female eastern chipmunks compete for different resources during the breeding season. We predict that the availability of breeding opportunities is a major factor setting male density, whereas female density is set by competition for other resources. This hypothesis was tested by removal of all residents of one sex or the other from experimental grids. When males were removed, survival of resident females was unaffected, density of females increased slightly because of recruitment, and large numbers of males from adjacent areas immediately moved onto the plot. When females were removed, male density and survival declined rapidly and a similar number of new females dispersed onto the plot. We conclude that breeding density in eastern chipmunks is set by adult females, probably on the basis of food resources. Adult females set their density independently of adult male availability. Adult males set their density by spacing behaviour according to density of breeding females.

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Introduction

Social spacing is a mechanism that guarantees access to limited resources and plays an important role in the regulation of animal populations (Chitty 1967, Watson and Moss 1970, Krebs and Davies 1978, Krebs 1985). Spacing behaviours maintaining social organization vary considerably among species as a function both of the mating system (Emlen and Oring 1977) and of the favorability of the environment (Barash 1974).

The eastern chipmunk (*Tamias striatus*) is a common and widespread diurnal sciurid inhabiting temperate forests in eastern North America. Population structure and density are determined by a loose form of territoriality maintained through agonistic encounters and encounter avoidance (Yahner 1978, Getty 1981a) but home ranges of residents overlap extensively and resource-rich patches are not exclusively defended. Population densities can vary considerably between locations and years, but the amplitude of fluctuations is

much less than that of many small mammals (Kirkland and Kirkland 1979).

Food supply is a major determinant of population demography in chipmunks. Supplemental food resulted in decreased home range size in eastern chipmunks (Mares et al. 1982; cf. Lacki et al. 1984) and in improved juvenile survival and growth and higher populations in Townsend's chipmunks (Sullivan et al. 1983). Food supply, however, may not be the prime objective of spacing behaviour for both sexes at all times. Males may differ from females in their resource priorities during the breeding season. Females assume all costs in the production of young and, thus, must obtain both a suitable burrow site and a sufficient food supply in a habitat that is temporally and spatially patchy. Males show no paternal behavior and, thus, incur no direct costs in rearing the young.

We tested the hypothesis that females compete with each other for space to ensure adequate resources for reproduction and that they establish their breeding den-

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Fig. 1. Diagram of the study site on the Oak Ridge's Moraine, northeast of Toronto, Ontario.

sities independent of male density. We test the hypothesis that breeding male density is dependent on access to resident breeding females. We tested these hypotheses by drastically altering the sex ratio through selective removal of adults of one sex or the other at the onset of early summer breeding activity.

Study area

The experimental plots were established in a 20 ha mature hardwood forest located on the Oak Ridge's Moraine, 40 km north-east of Toronto, Ontario. The terrain is hilly and well drained. The dominant species in the forest were sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*). Other species found in order of decreasing abundance include white ash (*Fraxinus americana*), basswood (*Tilia americana*), black cherry (*Prunus serotina*), red oak (*Quercus rubra*), butternut (*Juglans cinerea*) and white pine (*Pinus strobus*). The shrub understory was patchy and composed mainly of young sugar maple and common elder (*Sambucus canadensis*). The study site was surrounded mainly by old field, pasture, cultivated field, and, on the south, by a narrow pine plantation (*Pinus resinosa*). All trapping grids were established so that trap stations were at least 15 m from the forest edge.

Methods

Five live-trapping grids were established in autumn 1981 (Fig. 1): a Control grid; a grid from which all adult males were removed (Male-Removal); a grid from which all adult females were removed (Female-Removal); and two grids from which a few selected residents of

each sex were removed (Selective Male- and Female-Removal grids). The latter were set up to observe patterns of new recruitment or home range shifts of the remaining residents. All grids but the Female-Removal grid were located in a continuous woodlot and 140 m separated the Male-Removal from both Control and Selective Removal grids. Selective Removal grids were separated from each other by 40 m. The Female-Removal grid was located a minimum of 290 m from the other grids in an adjacent woodlot. The two woodlots were connected by two fencerows (Fig. 1).

Each grid was 2.56 ha in size with trap points arranged in a 7×7 pattern and spaced 20 m apart. One Longworth trap, baited with sunflower seeds and supplied with cotton bedding, was placed at each trap station. Live traps were locked inside a metal box to prevent disturbance by raccoons (*Procyon lotor*). Small mammals gained entry to the traps through a 2.54 cm diameter entrance hole in the metal box.

The study area was checked regularly for above ground activity of chipmunks from 15–18 March to mid-April but no activity was found. Snow covered the ground to depths of 50 cm on much of the area at that time. Each grid was trapped for 2 d every 7–9 d from 15 April to 31 October 1982. The traps were set at dusk and checked late in the morning of the following day and again in the morning of the next day. They were then locked open and left baited.

Animals were ear-tagged with numbered fingerling fish tags, and at each capture the following information was recorded: tag number, trap location, sex, reproductive status, and weight. Reproductive status in males was determined by testes position (scrotal or abdominal) and scrotal pigmentation. Breeding males show large testes descended into a darkly-pigmented scrotum (Smith and Smith 1972). Reproductive status in females was determined by the condition of the vaginal region (non-breeding, estrus, or post-estrus, depending on degree of swelling and colouration of the vulva; Smith and Smith 1975), by presence of lactating tissue, and by obvious pregnancy. Females may breed twice during the year. The first breeding period occurred in mid- to late March when the animals remained mainly in their burrows and were untrappable. The second breeding period occurred in late June to early July (Smith and Smith 1972, Tryon and Snyder 1973, Pidduck and Falls 1973, Smith and Smith 1975). It was during this second breeding period that we carried out our experimental manipulations. Animals were classified as adults (≥ 80 g) or juveniles (< 80 g) based on weight at first capture (Smith and Smith 1972, Pidduck and Falls 1973). Animals were defined as residents if they were caught at least three times on a grid before the removal experiments.

We used complete enumeration for our demographic analysis and calculated minimum estimates of trappability as an index of the efficiency of our trapping method (Krebs and Boonstra 1984). This estimate excludes the

Fig. 2. Reproduction of resident *Tamias striatus* on the Control and Male-Removal Grids.

first and last captures of an animal. Thus, animals caught only once, or twice in consecutive trapping sessions, were excluded.

Six other mammal species were captured on the grids and they are listed in order of decreasing abundance: short-tailed shrew (*Blarina brevicauda*), woodland jumping mouse (*Napaeozapus insignis*), white-footed mouse (*Peromyscus leucopus*), masked shrew (*Sorex cinereus*), long-tailed weasel (*Mustela frenata*), and northern flying squirrel (*Glaucomys sabrinus*).

Results

Trappability

Chipmunks on all grids were highly trappable with a mean trappability pooled over all grids of 80% for males (number of males in the population for more than two

consecutive trapping sessions = 46) and of 76% for females ($n = 49$). Even these trappabilities were probably underestimates as they include those trapping periods during the late summer when there was an above-ground lull in activity (Dunford 1972, Yahner 1978, Wrazen 1980, Lacki et al. 1984), as well as the trappabilities of animals whose home ranges only bordered on the study plots. Nevertheless, trappabilities were sufficiently high on all grids to make the demographic results reliable (Hilborn et al. 1976).

General population trends

We captured 263 chipmunks 1,390 times over a 22 wk period. Although traps were set three times from 15 April to 1 May, no chipmunks were caught before 5 May. Chipmunks were observed regularly between 18 April and 5 May, but they always appeared to be active only around burrow entrances and then only during periods of good weather. By the first week of October most adult residents had again become non-trappable. However, newly emerged juveniles of low body weight were caught until 31 October 1982. Before the removal of the animals from the experimental grids, the numbers were roughly comparable on all grids (Control - 15, Female-Removal - 20, Male-Removal - 23, Selective Female-Removal - 19, and Selective Male-Removal - 15).

Reproduction

At first capture in May, all adult males were in breeding condition and remained so until about the last week in July (Fig. 2). Adult females were more variable as some were lactating when first captured in May though most were not. These latter individuals presumably had not bred during the first reproductive bout earlier in the spring or they had lost their first litter. During the second or summer breeding period, most adult females came into estrus between 18 June and 14 July with a peak during the first week of July. Estrus was highly synchronous within a grid with all females on the Control ($N = 6$) being in estrus only during the last week of

Tab. 1. Total number of resident breeding females and new juveniles on all grids.

Grid	First breeding season			Second breeding season		
	Total resident females	Total juveniles caught	Juveniles caught per resident female	Total resident females	Total juveniles caught	Juveniles caught per resident female
Control	7	2	0.28	8	16	2.0
Female-Removal	11	7	0.64	—	11	—
Male-Removal	13	7	0.53	11	21	1.9
Selective	10	4	0.40	5	10	2.0
Female-Removal						
Selective	9	7	0.77	6	16	2.6
Male-Removal

Fig. 3. Minimum number of *Tamias striatus* alive on the three main grids. Vertical arrows indicate when the removals began. Population increases in September and October were the result of the appearance of juveniles.

June and the first week of July and 75% ($N = 12$) on the Male-Removal grid being in estrus in the first week of July. The removal experiments began immediately at the onset of this bout of sexual activity in females. Soon after estrus the adult females became non-trappable for several weeks. In the last week of July some lactating females again entered the trappable population. This appearance of lactating females about 4 to 5 wk after the first appearance of estrous females is consistent with the reported gestation period of about 31 d (Burt 1940, Pidduck and Falls 1973, Smith and Smith 1975). Throughout August and September, most (65%) resident females were again lactating in every trapping session, and by the end of September, nearly all adult females were again non-trappable and presumably hibernating.

Fewer females bred in spring than in summer, as indicated by lower numbers lactating (spring vs summer: Control grid – 28% ($N = 7$) versus 100% ($N = 8$) (Fisher's Exact Test, $P = 0.014$); Male-Removal grid – 37% ($N = 13$) versus 80% ($N = 11$) ($\chi^2 = 2.82$, N.S.) and by fewer juveniles produced (Tab. 1). Juveniles from the first breeding bout entered the trappable population from 20 June to 14 July and those from the second bout entered from 1 September to 31 October.

Male removal experiment

From 12 June to 13 July all adult males were removed from the Male Removal plot (Fig. 3). The 10 resident

breeding males were removed during the first 2 wk; thereafter, 28 non-resident adult breeding males (17 tagged animals from other grids and 18 untagged animals from elsewhere) entered the grid and were removed. Thus, 54% ($N = 11$), 25% ($N = 12$), and 40% ($N = 20$) of the males of the Control, Female-Removal, and the two Selective Removal grids, respectively, left their grids and moved onto the Male-Removal grid. Female numbers were not affected by the removals (Fig. 3), and survival was higher than that on the Control (Fig. 4). The expectation of life (Leslie et al. 1955) for breeding females present in June was 12.7 wk ($SE = 3.3$, $N = 7$) on the Control and 19.8 wk ($SE = 0.9$, $N = 11$) on the Male-Removal grid. Four new adult females (one tagged animal from the Control and three untagged females) subsequently moved onto this grid. Two new juveniles were also trapped shortly after the removals, but were caught only once. Thus, resident females were unaffected by the male removal. However, male removal may have created vacancies allowing recruitment of some adult females. On the Control grid during this time, only one adult female and one juvenile female entered the grid. The production of young on the Male-Removal grid was unaffected by the manipulation (Tab. 1).

Female removal experiment

From 18 June to 8 July, seven adults and one juvenile resident female were removed from the Female-Removal grid (Fig. 3). During the period up to 15 July, five non-resident adult and four new juvenile females moved onto this grid to replace the residents and were also removed. Immediately, adult resident males began disappearing (Fig. 3): three moved a minimum of 290 m to the Male-Removal grid and five were not caught

Fig. 4. Percent of *Tamias striatus* surviving on the three main grids. Percent values indicate minimum number of the resident cohort caught in the 2 wk period before the removal experiments that survived per 7–9 d. Number at the start of the period in parentheses.

again. We have no evidence of a sudden mortality factor to account for the disappearance of these animals and suspect that they may have dispersed into adjacent areas. Three resident males remained on the grid throughout the study period. Thus, removal of breeding females resulted in the disappearance of the majority of the breeding males, many of which moved to the Male-Removal grid. This disappearance of males from both the Female-Removal and the Control grid is reflected in similar survivorship curves (Fig. 4). The expectation of life for breeding males present in June was 8.9 wk (SE = 3.1, N = 8) on the Control and 8.8 wk (SE = 2.2, N = 10) on the Female Removal grid.

Eleven new juveniles appeared on this grid by the second week of October. These young were probably the offspring of breeding females with home ranges in adjacent undisturbed habitat.

Selective removal experiment

A few residents of each sex were removed from two adjacent grids to investigate the possibility that sex-specific replacement of removed animals would occur. However, the effects of the Male-Removal experiment so dramatically affected the males on the Selective Removal grids that recruitment trends were obscured. Four resident adult females were removed from the Selective Female-Removal grid on 23–24 June and five adult males were removed from the Selective Male-Removal grid on 19 June. In addition, three resident females disappeared from the Selective Male-Removal grid in the period subsequent to the removals. This may have been the result of predation, as two weasels (*Mustela frenata*) were captured and removed from this grid at this time, while no weasels were caught at any other time on any other grid.

The females removed from the Selective Female-Removal grid were replaced by only one new breeding female. As well, three new adult females and one juvenile female recruited to the Selective Male-Removal grid. Thus a total of twelve adult females remained on both grids combined. Of these, 10 were known to have reproduced in the second breeding bout. For the two grids combined, the ratio of new juveniles produced that summer to resident females was similar to that of the Control (Tab. 1). In summary, some compensatory female recruitment occurred but it was minimal.

Just after the removals, three of the adult males from the Selective Female-Removal grid and five adult males that had home ranges overlapping both Selective Removal grids moved to the Male-Removal grid. As well, three male residents of the Selective Male-Removal grid and two males which had home ranges overlapping both Selective Removal grids disappeared. No males replaced those removed from the Selective Male-Removal grid. Only seven males remained on both grids after the manipulations. Thus, selective removal of males did not result in immediate replacement by other males. In-

stead, the manipulations occurring on the Male-Removal grid had caused a major shifting by males on both Selective Removal grids. Similar proportions of males remained on the Control grid (27%, N = 11), on Selective Removal grids combined (35%, N = 20), and on the Female-Removal grid (25%, N = 12) ($\chi^2 = 0.42$, df = 2, N.S.) subsequent to the removals.

Discussion

Our manipulations had rapid and dramatic effects on the social structure of chipmunks. Resident breeding females were unaffected by the removal of resident males (Fig. 3), but male removal allowed some recruitment of new females into the resident population. In contrast, 75% of the resident males on the Female-Removal grid moved elsewhere. Similar results were obtained by Boonstra and Rodd (1983) in a polygynous microtine, *Microtus pennsylvanicus*. However, our results differ from theirs in that the removal of male voles from their male removal grid had no effect on the survival of males on their control grid. In our study, removal of male chipmunks from the Male-Removal grid caused many of the breeding males from all of the grids to move onto the Male-Removal grid. These differences may have been caused by differences between the studies in the physical arrangement of the grids and the distances among them, as well as by the greater mobility of male chipmunks relative to voles. However, unlike voles, in which females go through serial estrus periods throughout the breeding season that may last up to 9 months, chipmunk females only have two brief estrus periods. For voles, males on the control grids should not move to the male removal plot since they could expect further breeding opportunities with resident females. For chipmunks, once males have inseminated resident females in the second breeding bout, they may increase their reproductive fitness by searching for other estrus females. Thus, our Male-Removal grid became a localized female rich habitat for reproductive males. Any dominance hierarchy or territoriality between resident males that normally may develop in natural populations and act to restrict access to females by strange males, would not have had time to develop on our Male-Removal grid (Yahner 1978). Instead, there was an abundant and undefended resource that offered opportunities for mating far in excess of normal.

How did the males on the other grids detect that males were absent on the Male-Removal grid? Dunford (1970) suggested that "chipping", an agonistic vocalization, helps to maintain social organization. Subsequent to our removal of males, the absence of "male chipping" would rapidly communicate the absence of resident male competitors and thus intrusions could occur unopposed.

In natural chipmunk populations resident adults tend to be relatively evenly spaced as a result of territorial behaviour in the core areas of each animal, though

there can be considerable overlap in the overall home ranges of neighbouring residents (Dunford 1970, Tryon and Snyder 1973, Ickes 1974, Elliot 1978, Yahner 1978, Getty 1981a, b). Previous studies have shown that female chipmunks tend to have smaller home ranges than males though this largely reflects the tendency of males to increase the distance they travel from core areas during the summer breeding bout (Burt 1940, Yerger 1955, Ickes 1974, Yahner 1978). Males may maximize their reproductive fitness during the breeding season by maintaining a home range overlapping one or more females for which they will be able to monopolize access. With nearly all resident females available only during a brief 2–3 wk period each summer in which there is general synchrony in the time of estrus (Fig. 2), mating opportunities could be viewed as being temporally clumped and therefore females should be more likely to be defended by males. Local males may be able to detect estrus sooner thus preempting other males during a mating bout, or may be able to exert dominance on their own territory over other males. Such a system would be similar to that proposed by Farentinos (1972) for tassel-eared squirrels.

Distribution and abundance of food for chipmunks are spatially and temporally patchy (Forsyth and Smith 1973, Yahner 1978, Getty 1981a). Only by maintaining a fairly large home range and retaining some dominance over competing individuals within that range could a female guarantee sufficient food resources for reproduction. Production of young and lactation greatly increase the energetic requirements of female mammals above nonbreeding requirements (Kaczmarski 1966, Grodzinski and Wunder 1975, Millar 1979). Dunford (1970) and Yahner (1978) have shown that dominance over other resident individuals for a food resource diminishes with increasing distance from core areas. A fairly flexible hierarchy may develop between neighbouring females, with aggression being less severe between known neighbours than between residents and strangers, in a system similar to that found in other small mammals (Healey 1967, Thompson 1978). In this way, patches of superabundant food that periodically occur, such as the mast fall from a mature beech or oak, could be exploited easily by several neighbouring residents. Strangers would be excluded through aggressive behaviour of residents. Getty (1981b), through systematic behavioural observation, established that just such a social structure develops with minimal aggressive encounters between neighbours due to encounter avoidance behaviours. He found that 80% of aggressive encounters were with strangers. Evidence suggests that such a system of neighbour recognition may, in part, be based on identification of individual-specific odours (Halpin 1980, Keevin et al. 1981). Juveniles, upon approaching adult weight, would be forced to disperse by resident females in summer and by residents of both sexes in early autumn, in a system similar to that found-

in *Sciurus carolinensis* (Thompson 1978) and *Tamiasciurus hudsonicus* (Smith 1968, Rusch and Reeder 1978).

Chipmunk populations have been shown to respond to an increase in food supply by an increase in population density and a decrease in home range size (Mares et al. 1976, Sullivan et al. 1983) as well as by increasing juvenile survival (Sullivan et al. 1983). Though these findings suggest that chipmunk populations are food limited, they do not address the possible differences between the sexes in their response to increased food supply. Male density may have increased in response to increased food directly or it may have increased as a secondary response to increased female density.

We expect that our experimental manipulations should produce these same results at any time from the onset of the first above-ground activity in the spring until the end of the summer breeding period sometime in mid to late July. During this time, males should require food only for maintenance to allow them to pursue breeding activity. Thereafter, with no further opportunities for mating, the resource priorities of males should change and the focus of their behaviour should, like females, be the hoarding of food for overwinter use. Therefore, we could expect that from August until the end of above-ground activity in September–October there would be no effect on males of removing females.

Thus, we see two distinct periods during which density is set. Females set their density in the spring and summer to guarantee access to food and suitable burrow sites for reproduction and, in autumn, to retain access to food and to protect food hoards (Wrazen and Wrazen 1982) and overwintering burrow sites. Males set their density in spring and early summer to guarantee access to resident females, and, in late summer and autumn, to obtain food and to protect food hoards and overwintering burrow sites.

The fate of those chipmunks which cannot gain access to a home range is unknown. They may disperse to occupy marginal habitat as has been found in numerous species (Carl 1971, Krebs 1971, Van Horne 1982), though we currently have no evidence to suggest this. However, where all resident females were removed, only five new adult females moved in to replace them and where nine residents (four females and five males) were removed from the Selective Removal grids, four new adult females moved in to replace them. This suggests that there were a small number of surplus adult and juvenile individuals available for recruitment. Of the juveniles born during the spring breeding bout in 1982 (Tab. 1), few stayed for more than one trapping session. None remained on the Control (two were caught but did not stay) or on the Female-Removal grid (seven were caught of which five females near adult weight were removed). One juvenile male and one juvenile female remained on the Male-Removal grid for a minimum of four weeks. On the Selective Female-Removal grid of the four caught, one juvenile male and

one juvenile female remained for most of the summer and on the Selective Male-Removal grid of the seven caught, five juvenile males and two juvenile females remained for ≥ 4 wk, with five remaining until mid-September. Ickes (1974) found that juvenile chipmunks tended to remain in the vicinity of their birthplace well after their emergence and when all adult residents were experimentally removed it was these juveniles that tended to occupy the newly available core areas. Ickes did, however, find that a significant number of adult "floaters" were available to occupy the newly available core areas after residents were removed. However, when these experimentally removed residents were later released near their original home ranges, most reoccupied their core area within 8 d, thus forcing the dispersal of the new occupants.

A possible criticism of this study is that the low sample size on the grids could increase the probability of chance effects producing experimental artifacts. However, these densities are typical of eastern chipmunk populations in mature hardwood forest habitat throughout the range of this species (Yerger 1953, Forsyth and Smith 1973, Ickes 1974, Burt 1975, Elliot 1978, Lacki et al. 1984) and we trapped the majority of a large woodlot (20 ha). In addition, the results were so dramatic and consistent across all grids in terms of male movement onto the Male-Removal grid that it is unlikely it could have been produced by chance alone.

Further research to clarify the role of residents in regulating chipmunk populations through social behaviour is required. Radio-tagging of all juveniles known to have been born on the study site and a follow up on their activities and fates would indicate when the bulk of juvenile dispersal or mortality occurs. Accurate identification of maternity and paternity of juveniles would clarify whether related individuals of either sex are generally any more successful at establishing on a site than are strange individuals (Hankin and Sherman 1981, Tamarin et al. 1983). Further investigation is needed to determine if the frequency of successful paternity in the litters of resident females by resident males is greater than for males entering from elsewhere.

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