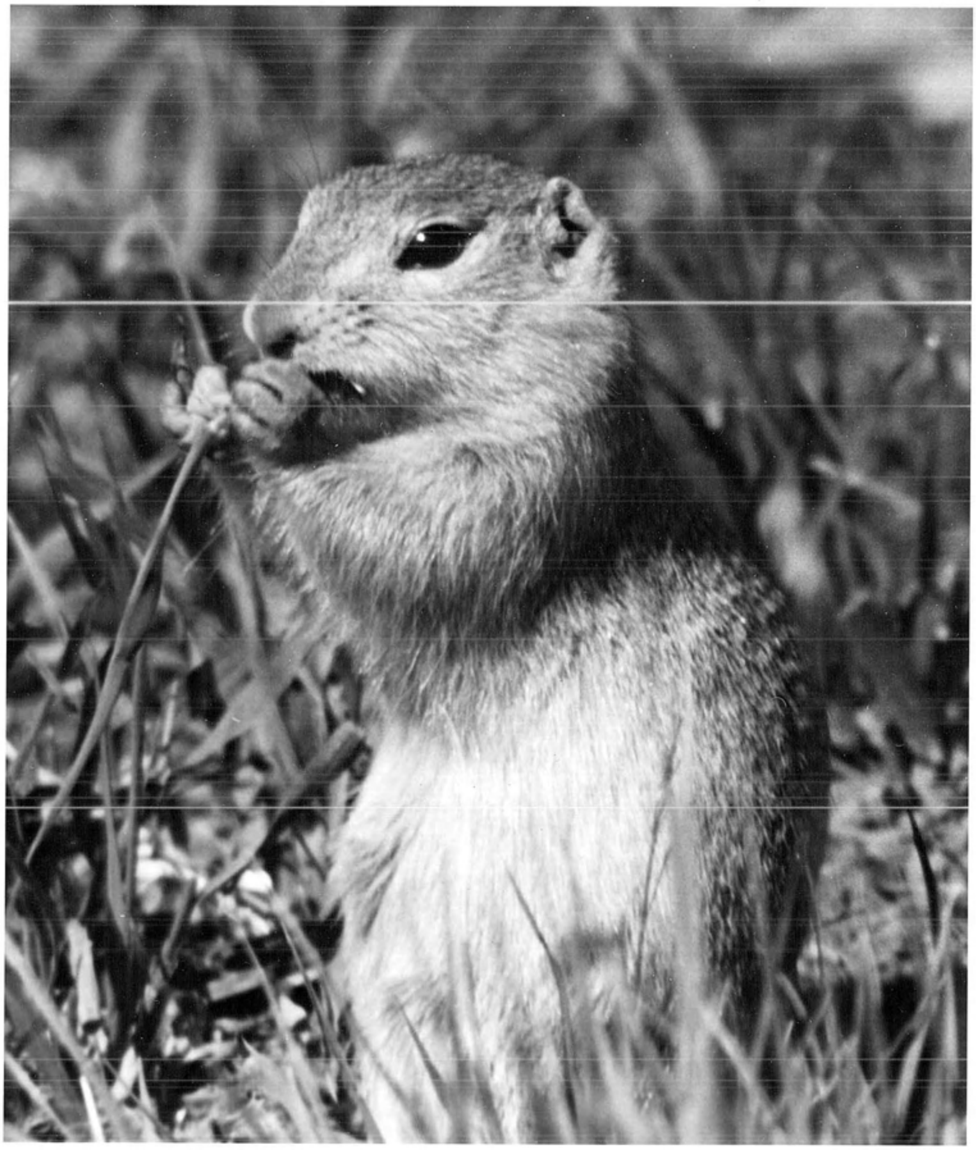

ASPECTS OF POPULATION DYNAMICS AND SOCIAL BEHAVIOR IN THE RICHARDSON'S GROUND SQUIRREL, AS MOFIFIED BY A CHEMOSTERILANT (MESTRANOL)

by

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Title of Thesis/~~Project/Extended Essay~~

Aspects of Population Dynamics and Social Behavior in the Richardson's Ground Squirrel, as modified by a Chemosterilant (Mestranol)

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ABSTRACT

This study measured the impact of a chemosterilant on the population dynamics and social behavior of Richardson's ground squirrels, and attempted to gain insight into general population control.

Plots were established in 1972 in Southern Alberta and different proportions of individuals in two populations were force-fed with mestranol. Squirrels were live-trapped, ear-tagged, dye-marked, weighed and released. Data on seasonal pattern of activity, population dynamics and social interactions were recorded throughout the summers of 1972 and 1973, and in April 1974.

Mestranol sterilized females in the year of treatment and influenced the onset of adult hibernation. Treated females immerged sooner than breeding females. Onset of hibernation for individual squirrels was influenced by population density and was related to breeding status, age, sex, initial body weight at emergence, and subsequent rate of fat accumulation.

Natality was greatly reduced by the treatment. In 1972, a reduced birth rate on the treated plots resulted in an increased immigration of non-treated adults and juveniles. Moreover, adults and juveniles on these plots were more successful in establishing residency than were squirrels on the control plot. In the fall of 1972, the treated plots had juvenile populations that were comparable to that of the control plot. In 1973, both adult and juvenile populations increased on the control plot. The two treated plots either maintained or saw a slight decrease of their adult populations; both plots failed to produce sizable juvenile cohorts. In April 1974, the treated plots had adult populations of 45% and 30% of the numbers first observed on these plots in April 1972; the control plot was left with 75% of its 1972 population.

Cohesive behavior among adults was rare and occured only between neighbours and related squirrels. Adult-young cohesive interactions were as frequent on the treated plots as on the non-treated plots. However, 85% of adult-young interactions were observed between mother and offspring on the control plots, while 43% of such interactions occured between juveniles and non-related adults on the treated plots. Cohesive behavior among juveniles could not be related to treatment. More cohesive interactions were observed among littermates than between non-related juveniles.

Agonistic behavior was frequent among adults. In a year of 'poor' vegetation conditions, differences in adult agonistic behavior were related to treatment and to population density. The treatment reduced the levels of aggression of the treated squirrels, while higher population densities were related to a higher frequency of agonistic behavior among breeding adults. No such differences could be measured in a year of 'better' food supply.

The size of core areas was the same for treated and non-treated squirrels, but overlap was greater on the treated plots. Core areas were larger on plots with low numbers of squirrels than on plots with high numbers. Changes in climatic and vegetation conditions modified the core areas' distribution and overlap, but did not significantly alter their size.

Levels of adult-young agonistic interactions did not differ between treated and non-treated plots, although treated adults never behaved aggressively towards juveniles. On non-treated plots, adult-young aggression increased with rising densities. Such a relationship was partly shown on the treated plots.

In 1972 no relationship could be established between levels of juvenile (young-young) agonistic behavior, juvenile densities and the treatment given. However, littermates were less aggressive to one another than they were to non-related juveniles. In 1973, a drastic decline of the juvenile numbers born on the treated plots showed that below a certain density, juveniles cease to interact agonistically to one another. A higher juvenile density on the control plot in 1973 was characterized by a higher frequency of agonistic interactions among littermates.

Sterilization changed the breeding status of treated squirrels and modified adult and juvenile densities. Within limits, levels of agonistic behavior, spatial and temporal distribution of the squirrels changed in response to population density increases or decreases which were related to the treatment or to natural causes.

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INTRODUCTION

For many years, a controversy has raged as to whether animal populations are regulated by extrinsic factors such as weather (Andrewartha and Birch, 1954), parasitism, predation, disease, food shortage (Nicholson, 1933), or a combination of all environmental factors (Thompson, 1956). Alternatively it has been suggested that populations regulate themselves through intrinsic factors such as social behavior, or through physiological and genetic changes which cause a population to adjust its density to prevailing environmental conditions (Wynne-Edwards, 1959 and 1962; Christian and Davis, 1964; Chitty, 1967). Some evidence has been gathered on both sides of this argument, i.e. environmental control of populations versus self-regulation, but at the present time, neither theory can be dismissed, nor can the possibility that a combination of both types of factors may be regulating animal populations.

Much work has been done on the behavior and population biology of the genus _Spermophilus_, a group of ground-dwelling sciurids (MacClintock, 1970), and different mechanisms of population control were shown or hypothesized to be at work in the different species. McCarley (1966) suggested that dispersal of the juveniles was the most important regulatory factor in populations of the thirteen-lined ground squirrel (_S. tridecemlineatus_). Similarly, density-dependent dispersal of the juveniles, and to a lesser degree density-dependent predation by badgers, control populations of Uinta ground squirrels (_S. armatus_) (Balph, 1970; Slade, 1971; Slade and Balph, 1974). In the same species, Burns (1968) demonstrated that agonistic behavior was an important means of population regulation, especially for juveniles but also for adult and yearling squirrels. In the artic ground squirrel (_S. undulatus_), territoriality and the availability of suitable hibernation burrows may limit the populations (Carl, 1971). Overwinter mortality was thought to be the main controlling factor in populations of Franklin's ground squirrels (_S. franklinii_) (Iverson and Turner, 1972). Fitch (1948) believed that predation, food supply and weather controlled populations of the California ground squirrel (_S. beecheyi_). In the round-tailed ground squirrel (S. tereticaudus), dispersal of adults and juveniles was correlated with onset of territorial behavior, but behavioral factors were not sufficient to limit squirrel density when food was abundant and predation rate was low (Dunford, 1977a).

A number of population studies have been made of the Richardson's ground squirrel, Spermophilus richardsonii richardsonii (Sabine, 1822), and not all agree as to the control mechanisms at work in this species. Yeaton (1969 and 1972) and Wehrell (1973) assumed that juvenile dispersal was a major contributing factor in population reduction, although juvenile dispersal and social aggression did not seem to be related (Yeaton, 1972). Overwinter mortality was thought to be fundamental to population regulation by Clark (1970) and D.R. Michener (1972), with dispersal and predation (Clark, 1970) being of lesser importance. Michener (1972) postulated that overwinter mortality was determined by weather and by the variety of hibernation burrows being used such that in a mild winter, greater numbers of ground squirrels in marginal habitats survive. Michener (1973c) dismissed intraspecific fighting as a possible cause of mortality in Richardson's ground squirrels. Finally, Dorrance (1974) after 4 years of field work on control and experimental populations of Richardson's ground squirrels showed that the annual numbers of adults were primarily determined by juvenile mortality between birth and emergence from the maternal burrow, and by overwinter mortality; both of these factors were ultimately determined by the quality of vegetation, which in turn was dependent on weather. He considered that predation and dispersal were of minor importance.

These previous studies have suggested that juvenile dispersal, overwinter mortality, availability of hibernating or breeding burrows as determined by aggressive behavior or weather, weather itself and its influence on food suppply and mortality, and finally predation are possible mechanisms of control in populations of Spermophilus. In some cases, one or more factors are regarded as primordial by one researcher, but are dismissed by another, and this sometimes within the same species. In Richardson's ground squirrel, juvenile dispersal and mortality, overwinter mortality and weather are the factors mentioned by many researchers as being the most important.

For many years, ecological studies were mostly descriptive and when relationships were established, they could not be supported with quantitative data. However new approaches are now being explored, one being the experimental modification of populations as advocated by Krebs (1978). By altering one factor in a given population, it is likely that others will be modified. By measuring such changes, cause and effect relationships may be established. Such modifications are commonly done by government agencies and others when attempting to control urban or agricultural pests. Since the late 1960′s, biological control involving the disruption of a biological process rather than the use of ′conventional′ techniques, has been advocated as a safe and effective way of controlling vertebrate pests (Howard, 1967).

Following this rationale, the Alberta Department of Agriculture initiated field research projects to assess the impact of chemosterilants on populations of Richardson′s ground squirrels (Biggs, 1970; Yaremko, 1972; Goulet and Sadleir, 1974). This species is considered to be an agricultural nuisance in Alberta (Brown and Roy, 1943). A chemosterilant is defined as being ′a chemical that can cause permanent or temporary sterility in either or both sexes or, through some other physiological aspect, reduce the number of offspring or alter the fecundity of the offspring produced′ (Marsh and Howard, 1970). Biological control implies the disruption of a biological process, in this case the disruption of breeding by a chemosterilant. Harper (1969) and Balser (1964) reviewed chemosterilants in current use and considered their advantages and disadvantages in regard to control of vertebrate pests. Mestranol was shown to efficiently reduce fecundity in rats and voles (Howard and Marsh, 1969; Marsh and Howard, 1969; Storm and Sanderson, 1970). By applying this chemosterilant to populations of Richardson′s ground squirrels, it was hoped to determine if mestranol could successfully reduce squirrel populations.

The present study used the same means and had the same goal, but also attempted to discover the ecological implications of such a treatment. Most importantly, it was hoped that mechanisms of population regulation would be revealed, especially with regard to the social behavior of these populations. Based on the information already gathered by other researchers, and on the data accumulated during the present study, I will attempt to determine the factors affecting the population levels of the

Richardson's ground squirrel, and to ascertain the role played by aggressive behavior in the regulation of these populations. First, the effectiveness of mestranol as a chemosterilant will be examined (Part I), and its influence on the local annual cycle of the species will be determined (Part II). But most importantly, the impact of the treatment on the population dynamics (Part III) and on the social behavior (Part IV) of the treated populations will be assessed. A general discussion will attempt to link all these aspects and to relate the resulting conclusions to current theory of animal population regulation.

THE STUDY AREA

A. General description

A study area in the vicinity of Youngstown, Alberta (51° 32′ N, 111° 13′ W) was chosen because Richardson′s ground squirrels were plentiful in the area. Colonies abound in this semi-arid short grass prairie which is characterized by few poplar groves, numerous sloughs and an undulating topography. Twenty percent of the solonetzic soils are potentially arable while the remaining land is used as pasture for cattle (Government and University of Alberta, 1969). Ground squirrels are found mainly along ridges and knolls where the soil is dry and vegetation short.

Very little of the original native vegetation remains undisturbed. Most dry lands were cultivated during the early 1900′s and were subjected to soil drift and wind erosion during the drought of the thirties (Bird, 1961). Consequently the pasture vegetation is now a mixture of weeds (Frankton and Mulligan, 1955) and native, and introduced plants (Moss, 1955). Grasses (Best et al., 1971) such as wheat grass (*Agrostis* sp.), porcupine grass (*Stipa* sp.) and blue grama (*Bouteloua* sp.) are dominant. The weeds and native plants are widely distributed while shrubs, such as the wild rose (*Rosa* sp.) or snowberry (*Symphoricarpos occidentalis*), and trees such as willows or poplars are less common and sporadically distributed (App. 1).

In spite of its desolate aspect, the area abounds in wildlife. Jack rabbits (*Lepus townsendii campanius*), pronghorn antelope (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) are commonly seen in pastures while numerous shore birds and ducks reside in the sloughs. A number of potential predator species of ground squirrels are present, such as coyotes (*Canis latrans*), badgers (*Taxidea taxus*), long-tailed weasels (*Mustela frenata longicauda*) (Banfield, 1974) and hawks - *Buteo jamaoansis*, *B. swainsoni* and *B. regalis* (Godfrey, 1967).

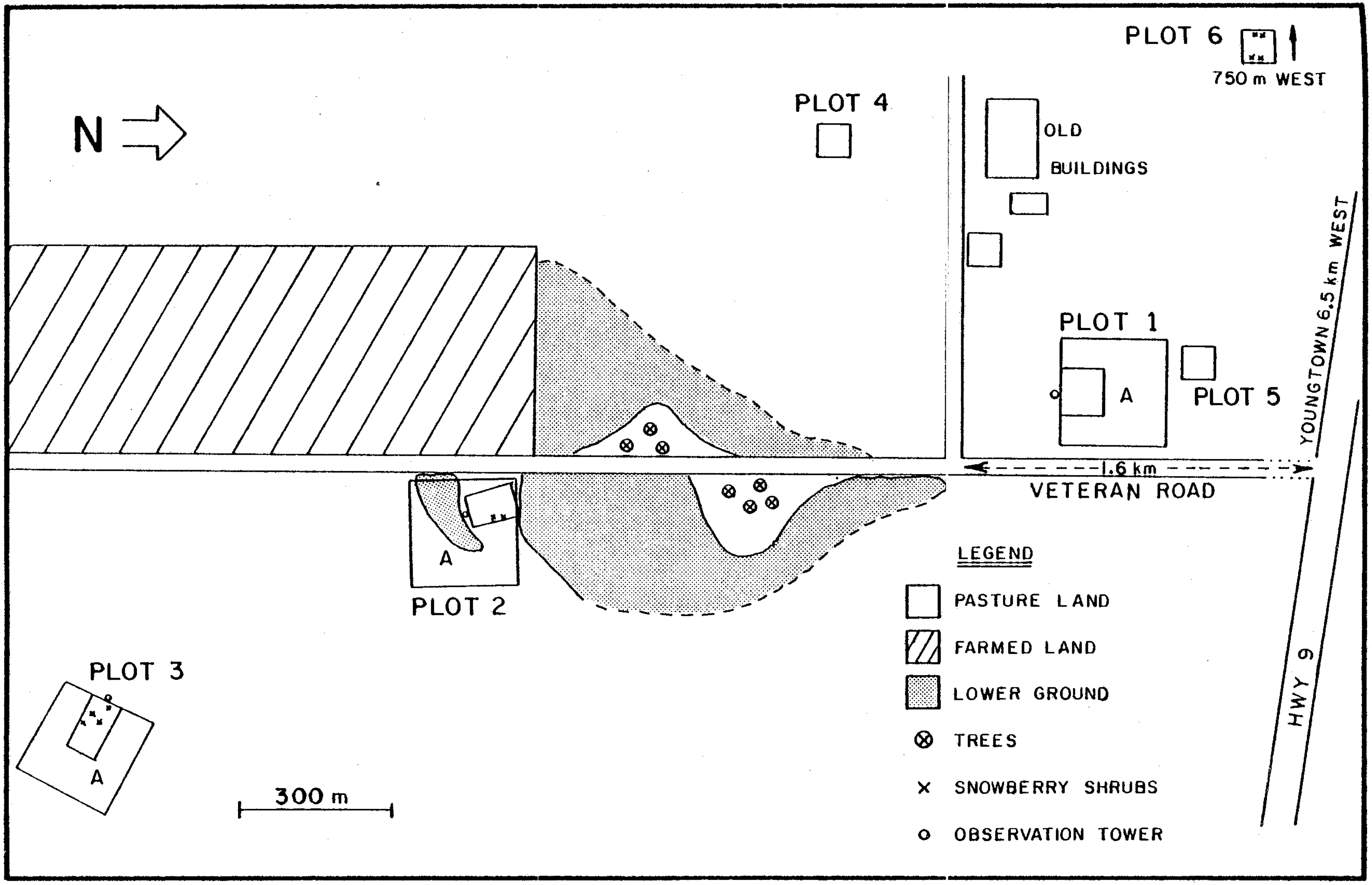
B. Plot description

In March 1972, three observation plots were established in separate pastures where grazing pressure from cattle was roughly the same. In each plot ground squirrel populations were higher than in the surrounding pasture. The plots were located at least half a mile apart to reduce the probability of squirrel movement from one plot to another. Soils and vegetation were similar in all plots, except that snowberry was negligible in plot 1 and abundant in plot 3 (Fig. 1). The area of short grass components were roughly equivalent in all plots and plots were located so as to include a maximal number of occupied burrows. Plot 1 was square and measured 0.65 hectare, while plots 2 and 3 were rectangular and measured 0.69 and 0.81 hectare respectively (Fig. 1). Each of these plots was surrounded by a larger 4-hectare plot (1A, 2A, 3A) in which squirrel density was determined by trapping (Fig. 1).

After the plots were established and observations started, certain differences became apparent. Plot 1 was a winter feeding ground for cattle; seeds were left in the spring after snowmelt providing an early source of food for emerging squirrels. Plot 2 was surrounded by lower land where tall grasses were growing (Fig. 1). This lower area was not suitable for burrowing, as it was too wet and offered poor protection from predators for quirrel visibility was reduced by the tall vegetation. However, it was an important source of food and nesting material during the summer. Well beaten paths led from the colony to this area.

Three 1-acre plots (0.40 ha), plots 4, 5 and 6, were established during the later part of May 1973. Plots 4 and 5 were vegetatively very similar to the control plot (#1), while plot 6 resembled plot 3 in containing snowberry bush. Plots 4, 5 and 6 were located in areas of high squirrel densities in relation to the surrounding ground but were not such well defined colonies as plots 1, 2 and 3. Burrows were less numerous in plots 4, 5 and 6 than in plots 1, 2 and 3, and were surrounded by smaller mounds. A continuum of low density populations were observed around plots 4 and 5 whereas plot 6 was more isolated. This latter plot was joined on two sides by cultivated fields which were devoid of ground squirrel populations.

Figure 1. Location of the six plots used during a Richardson's ground squirrel study made between March 1972 and April 1974 near Youngstown, Alberta.


N
PLOT 4
PLOT 6
750 m WEST
OLD
BUILDINGS
YOUNGTOWN 6.5 km WEST
PLOT 1
A
PLOT 5
1.6 km
VETERAN ROAD
A
PLOT 2
LEGEND
PASTURE LAND
FARMED LAND
LOWER GROUND
TREES
SNOWBERRY SHRUBS
OBSERVATION TOWER
HWY 9
PLOT 3
A
300 m

MATERIALS AND METHODS

A. Trapping and marking

In March and April 1972, the three 4.0-hectare plots surrounding plots 1, 2 and 3 were intensively trapped to estimate the density of squirrels in these areas. From March to September 1972 and 1973, and in April 1974, all ground squirrels observed within the three central plots, or close to their boundaries, were captured with a nylon noose or a National Live Trap (P.O. Box 302, R.R. 1, Tomahawk, Wisc.). Each squirrel was weighed (to 5 g) and its sex determined. Signs of pregnancy or lactation were recorded for females; swollen nipples indicated a state of advanced pregnancy or lactation. For males, the degree of enlargement of testes and colour of the scrotum were noted; injuries and scars were also recorded. All squirrels were individually identified with a numbered ear tag and a permanent black fur dye (Nyanza Inc., Lawrence, Mass.). If it became necessary, squirrels were recaptured for marking so that their individual dye patterns were always recognizable. Trapping was avoided at the time of parturition. Squirrels remained in the traps usually for less than 10 minutes and were put in the shade as soon as caught. All squirrels were released near the burrow where they were first caught immediately after marking. There were no deaths caused by trapping. Similarly, all squirrels present within or near the boundaries of plots 4, 5 and 6 were captured during the later part of May 1973, and were weighed, sexed, ear-tagged and dye-marked.

Three age classes were recognized: 1. juveniles, aged less than 12 months, 2. yearlings, aged from 12 to 24 months, and 3. older adults, which were 24 months and older or were not marked when first captured. Squirrels first trapped in April 1972, and non-marked squirrels trapped in April 1973 and 1974 were all classified as adults although some could have been yearlings. It was not possible to distinguish the yearling from the older squirrels by either the body weight or fur colour. Squirrels born in the plots in 1972 and 1973 were easily identified by their small size and weight and by a different fur colour. They were classified as juvenile from the time of their birth until they were 12 months old.

Numbers were given to the different groups of ground squirrels trapped between 1972 and 1974 for ease of reference when discussing age composition or annual survival. The following age classes were defined:

1. adults of unknown age, i.e. 1 year+, first trapped in 1972. 1a refers to some of these adults that were trapped in April 1972
2. juveniles born during the summer of 1972
3. adults of unknown age, i.e. 1 year+, first trapped in 1973. 3a refers to those trapped in April 1973
4. juveniles born during the summer of 1973
5. adults of unknown age, i.e. 1 year+, first trapped in 1974. 5a refers more specifically to those trapped in April 1974

B. Mestranol treatment

Squirrel populations were treated with mestranol in early April 1972 and 1973. The drug was generally given before breeding, or at least in early pregnancy. Each treated squirrel was force-fed a 1 mg dose of mestranol (Sigma Chemical Co., 3500 De Kablst, St. Louis, Miss. 63118) dissolved in 1 ml of peanut oil. Squirrels were kept under observation in the shade for about 15 minutes after they were treated and none were observed to regurgitate.

In an attempt to limit ingress into the plots by juveniles or adults from nearby outside areas, mestranol baits (1 mg of mestranol dissolved in 1 ml of peanut oil and mixed with 5 g of rolled oats) were distributed at the entrances of burrows within a 300-foot distance from the boundaries of plot 2 in 1973. In a similar attempt to reduce immigration, force-feeding was used around plot 3 in April 1972. However, this was very time-consuming since all squirrels had to be captured. The rationale for this procedure was that if neighbouring females were sterilized, fewer juveniles would be born and thus be available to move into the plots.

Three previously untreated squirrels were administered the drug on plot 2 in May 1973 to determine the effect of mestranol on lactating females and their offspring. Three juveniles were also fed the drug in June. Finally, eleven adults were trapped, marked and force-fed with mestranol (1 mg) in areas well away from the plots. Six of these squirrels and 15 non-treated adults were later killed and their gonads were preserved in 10%

formalin for histological analysis.

Plot 1 was kept as a control since no squirrels were treated in 1972 or 1973 (Table 1). Each year, roughly half of the females were treated on plot 2, while nearly all females were treated on plots 3 in 1972 but none were in 1973. This difference in the treatments was established to compare treated and non-treated populations and to assess the success of a 2-year 50% treatment to control squirrel populations in comparison to a 1-year 100% treatment. Also the presence of two equal size groups of treated and non-treated squirrels in a same population permitted determination of possible impacts of the treatment on these squirrels, regardless of any other environmental factors. Supposedly all external factors were the same for all squirrels belonging to that population.

Table 1. Mestranol treatment given in April 1972 and 1973: percentage of the female population treated with 1 mg of mestranol.

	Plot 1 (control)	Plot 2	Plot 3
April 1972	0% n=18	53% n=15	78% * n=9
April 1973	0% n=33	56% n=16	0% n=14

n: total number of females present in plot in April
*: an attempt was made at treating all squirrels in this plot, but 2 females escaped capture until it was too late to treat them.

C. Behavioral observations

Plots 1, 2 and 3 were subdivided into a grid of 10 m x 10 m quadrates marked with numbered sticks. Observations were made from 16-foot high towers using binoculars (8x32 Leitz) or a telescope (Bushnell, 15x). Behavioral observations were made from April 21 to August 12 in 1972 (156 45-minute periods), and from April 16 to August 28 in 1973 (78 45-minute periods) on plots 1, 2 and 3, and also between June 2 and August 28, 1973 (64 45-minute periods) on plots 4, 5 and 6 (App. 2). The three 0.40-hectare plots (4,5, 6) were not subdivided. In these plots, squirrels were individually identified at each observation period and their location recorded as being in one quarter of the plot, e.g. S.W. corner, and in relation to landmarks such as bushes, mounds, etc. Observations on plots 4, 5 and 6 were made from the roof of a pick-up truck. An equal amount of time was spent observing animals on all plots and the 45-minute observation units were rotated throughout the day between 8 A.M. and 6 P.M. (App. 2). Midday hours were avoided when the temperature was higher than 80°F in a nearby Stevenson screen because ground squirrel activity was reduced at such times.

In 1972 and 1973, in each of plots 1, 2, and 3, all visibly active squirrels were noted at 15-minute intervals during 45- minute observation periods. The position of each active squirrel was plotted on a gridded map of the site. Three perimeter lines were drawn by eye to enclose the minimal area that encompassed 50%, 75%, and 95-100% of all activity sites of each squirrel. The area containing 50% of the activity sites of one squirrel is called the 'core area' of that squirrel (Michener, 1979), and the area containing 95-100% of sites is called the 'home range'. The home burrow was always included in the core area.

Not all of the areas between outermost activity sites were necessarily part of the home range. Squirrels frequently used narrow corridors between areas to circulate through the colony to a dug-out or to a source of nesting material. Up to 5% of observed activity sites (those 30 m or more from the 75% enclosure line) were judged to fall outside the activity range of the resident animal, and were excluded from the estimated home range. A minimal area enclosing 50%, 75% or 95-100% of the points was chosen here each time rather than the typical polygonal home range. It was shown by Recht (1977) in a radiotelemetry study of the Mohave ground squirrel that the home range consisted of an arterial network of pathways.

The following social interactions were recorded during the present study:

Cohesive Interactions

1. NOSE-TO-NOSE, NOSE-TO-BODY, NOSE-TO-ANUS: all forms of recognitive behavior where one animal touches another (Michener, 1972; Wehrell, 1973, Yeaton, 1969). These interactions were recorded as being cohesive when they were not followed by other interactions, either cohesive or agonistic.
2. KISS: nose-to-nose contact with one or both animal's mouths open (Quanstrom, 1968; Sheppard and Yoshida, 1971; Wehrell 1973; Yeaton 1969). This interaction was mostly observed between littermates or between mother and young.
3. SOCIAL GROOMING: one animal grooming another, or both animals grooming each other (Michener, 1972; Quanstrom, 1968; Sheppard and Yoshida, 1971; Wehrell, 1973; Yeaton, 1969).
4. PLAY: this consisted mostly of play-fight and play-chase behavior and was described in detail by Quanstrom (1968) and Yeaton (1969). During this study, this type of behavior was observed mostly between littermates.

Ground squirrels, like many other animals, maintain a certain distance between themselves and others. When another squirrel enters this space, or individual distance (Hediger, 1950), they react by attacking or retreating. However, certain classes of squirrels, (mostly littermates, mother and young or neighbouring adults) were observed within this individual distance and did not react either cohesively or adversely to each other. This distance varied during the season as the frequency of agonistic behavior changed for adult and juvenile squirrels. Squirrels were said to be in a positive association when they were observed to be peacefully present within a distance that elicited aggression between other squirrels at that same time of the season.

Agonistic Interactions

1. AVOIDANCE, MUTUAL AVOIDANCE: one animal approaches another but stops before contact. The hair on the tail is erected and one or both animals withdraw (Sheppard and Yoshida, 1971; Wehrell, 1973).
2. THREAT: usually directed towards an approaching animal. May be reciprocal. The back is slightly arched, the tail fluffed out and held stiffly behind or at a slight upward angle; the head or sometimes posterior are directed towards the approaching animal, one forepaw held rigid and directed ahead. The anal pappillae are frequently extruded (Michener, 1972; Sheppard and Yoshida, 1971; Wehrell, 1973; Yeaton, 1969).
3. FACE-OFF: reciprocal threat between two animals with both remaining on one spot or circling in the direction they are facing (Quanstrom, 1968).
4. CHASE/ESCAPE: chasing occurs either following a threat or other agonistic interactions when one animal attacks an intruder which then runs away. A chase varies from a few feet to over 100 feet and can be followed by other agonistic interactions if the chaser overtakes the animal chased, or ends when the dominant animal stops chasing (Michener, 1972; Quanstrom, 1968; Wehrell, 1973; Yeaton, 1969). Reversal was common during a chase.
5. FIGHT: while fighting, the two animals lock together, roll over and over and bite each other (Michener, 1972; Sheppard and Yoshida, 1971; Wehrell, 1973; Yeaton, 1969). Two intensities of fighting were recognized during the present study. The "fight sec" lasts from 1 to 3 seconds as one of the squirrels immediately flees; the "fight"lasts much longer as both animals participate actively and repeatedly jump at each other. Serious wounds were seen on adult males in early spring as a result of this latter type of fighting.
6. BITE: G.R. Michener (1972) describes this type of agonistic interaction as being a rare contact where one squirrel quickly bites the other without any subsequent agonistic contact. This interaction was not unusual during the present study and occurred when an adult female sought to prevent a juvenile from entering her core area.

All social interactions seen during each 45-minute observation period were recorded as to their nature, outcome, location within the plot, and the interacting squirrels were identified whenever possible. Interactions were seen to occur singly or most often in combination with others. Individual interactions or a sequence of interactions were indentified as such and counted as 'one' for quantification purposes. If a reversal occurred during an interaction, ie. squirrel A first chases squirrel B and then is chased by squirrel B, the interactions were counted as 'two'. The interaction rate was standardised as to density and time in the following manner: 1. The whole period of study was divided for each year into 10-day periods, numbered from 0 to 13 starting April 10 (App. 2). 2. The total number of cohesive and agonistic interactions observed were summed separately for each 10-day period (App. 3 and 4), and were divided by the number of 45-minute observation periods made during a given 10-day span (App. 2). 3. The maximum number of different squirrels observed within a plot was counted for all 45-minute periods and averaged for each 10-day period (App. 5). 4. For a given 10-day period, the average number of cohesive or agonistic acts per 45-minute period was divided by the corresponding average number of squirrels then active in the plot. 5. This number of cohesive or agonistic acts per squirrel, per 45-minute period was then multiplied by 100 for every 10-day period. Such figures could thus be used to compare plots, years and groups of squirrels, and to follow changes in the levels of social behavior throughout different seasons and years. An example calculation is given in Appendix 6.

Finally, sky cover, wind speed and the occurrence of precipitation were recorded for each observation period. The presence and identity of predators within or near the plots were also noted during observations. Predators such as weasels were trapped and removed from the plots whenever they were observed.

In the entire section on behavior, the following abbreviations will designate the different squirrel groups: A: non-treated adult squirrels, M: mestranol-treated adult squirrels, Y: juvenile squirrels less than one year of age. The Y class includes Yborn, which are juveniles born within the plots boundaries and Yout, which are juveniles born outside the plot boundaries. Interactions among the different groups of squirrels will be recorded accordingly. AA indicates interactions between non-treated adult squirrels. AM and MA interactions were observed between non-treated and treated squirrels, the first letter indicating which type of squirrel is dominant, i.e. won the interaction. MM identifies the interactions which occurred between two mestranol-treated adult squirrels. AY specifies interactions observed between non-treated adult squirrels and juveniles that were not their offspring. AownY indicates acts between an adult female and her offspring. Similarly, MY, YY and Litt. indicate interactions between mestranol-treated adult squirrels and juveniles, between juveniles that were not known to be related, and between juveniles that belonged to the same litter.

D. Other procedures

Plants found within the plot boundaries as well as plants not present on the plots but otherwise characteristic of the area were collected for identification. The resulting plant list is by no means exhaustive but represents the dominant species found in the area (App. 1).

Weather was recorded during the periods March to September 1972 and 1973; rain and snow falls were noted as well as wind velocity (personal scale) and maximum-minimum temperature (Stevenson screen). Cloud cover was also noted (App. 2).

Statistical tests used are the Student's T-test, used mostly to compare weights; the Mann-Whitney ranking test used to compare behavioral data, and the chi-square test (with Yates correction) used for population dynamics data (Clarke, 1969; Zar, 1974). Whenever a statistical test is used to compare data values, the test name is specified and the level of significance is indicated. N.S. means that level of significance is not reached - here 95% or $p < 0.05$. S.95, S.97.5, S.99, etc. indicate the level of significance of a given comparison. When a 'zero' value is encountered for a chi-square test, the zero is replaced by "1" for calculation purposes, so as to always minimize the difference observed between two proportions. The Mann-Whitney and the chi-square tests which are both non-parametric tests were chosen to analyze most of the results as they make no assumptions about the distribution of the populations sampled.

RESULTS PART I. EFFECTIVENESS OF MESTRANOL AS A CHEMOSTERILANT

A. On recruitment

In early April 1972, 20 adult females on plots 2 and 3 were given 1 mg of mestranol; 15 of these females remained in May of which two were lactating (App. 7). One of these latter females succeeded in raising a single juvenile. The normal mean litter size of the species is 6.92±0.18 (S.E.) in Saskatchewan (Sheppard, 1972) and from 3.7 to 6.3 juveniles emerge for each female in central Alberta (Dorrance, 1974). Three additional females captured outside the plots and similarly treated in April 1972 also failed to reproduce. All 9 females treated on plot 2 in April 1973 did not reproduce. Of a total of 27 adult females treated in early April 1972 and 1973 and still present at the time of parturition, only one succeeded in raising a much reduced litter.

Six of the 20 females treated on plots 2 and 3 in April 1972 were recaptured in 1973; all were palpably pregnant (App. 7). Two were treated again with mestranol, one in early April, the other in early May when lactating; no young were observed above ground with either female. The four remaining females all lactated in early May but only two of these were observed subsequently with litters of 2 and 1 juveniles (App. 7).

Additional squirrels were given mestranol in early May 1973. On plot 2, three lactating, previously untreated females were given 4 mg of mestranol (two 2 mg doses, two days apart). Only one was later observed with a single young. These procedures were designed to determine the effect of mestranol on suckling ground squirrels, as it was known in voles that mestranol can be transmitted through the mother's milk (Rudel and Kincl, 1966). However most juveniles died and the only juvenile surviving, as well as 3 other juveniles force-fed with 1 mg of mestranol in June 1973, were not recaptured in 1974.

Although many females were still present in May in the areas surrounding plot 3-1972 and plot 2-1973, very few juveniles were observed. This is assumed to be a consequence of the April mestranol treatments given around these two plots (force-feeding around plot 3, rolled oat baits around plot 2), as some of the females most likely never gave birth after being force-fed with mestranol or taking the bait. However, no accurate measurement of the effect of the treatments was obtained for these populations.

B. Histological evidence

Three females treated in early April 1972 were captured and killed 1 to 3 weeks following the treatment. None was lactating and histological preparation of their reproductive tracts showed that two females had all embryos resorbing while the other had necrotic placentae and dead embryos in utero. Ten non-treated females were killed at the same time; all had viable embryos. A single female treated with mestranol in April 1972 that did not reproduce that year was found to be pregnant with 5 viable embryos the following year.

Mestranol did not seem to affect adult males; histological sections of testis did not show any difference between treated (n=2) and non-treated (n=5) males. However, the sample size was very small and a more extensive collection of gonads from treated males might show some effect. All males recaptured in early May had regressed testes whether or not they had been treated in early April.

C. Summary

Mestranol was effective in temporarily sterilizing almost all females (96%) treated in early April. The 1 mg treatment given in April 1972 sterilized adult females for one breeding season, and may have been the cause of the loss of, or reduction in, litter size for the year following the treatment. However, this secondary effect can not be definitely attributed to the mestranol treatment. Mestranol did not seem to affect lactating females when given in a 4 mg dose but possibly provoked the death of most juveniles suckling these females. No effect of mestranol (1 mg) could be shown for adult males.

RESULTS PART II. ANNUAL CYCLE

Captures and recaptures of 406 different squirrels as well as periodic visual observations on the study area during the period March 1972 to April 1974 permit a description of the annual cycle. The timing of some events was determined directly through visual observations or trapping, while for other events, timing was determined through both of these means and through calculations based on other researchers′ findings. Only observed events are presented in Table 2.

A. Emergence of juveniles, parturition, breeding and emergence from hibernation.

The first event in the annual cycle that was observed accurately and for which mean dates could be established was the emergence of the juveniles from the maternal burrow. All young squirrels emerged between May 8 and June 5 in 1972, and between May 11 and May 21 in 1973; the average dates of emergence for juveniles were May 20 (n=22) (median is May 19) and May 17 (n=14) (median is May 17) in 1972 and 1973 respectively (Table 2).

Young squirrels remain in the maternal burrow for about a month before they are first observed above ground (Quanstrom, 1968; Michener, 1977). This was corroborated by my own observations: a litter of juveniles was observed to emerge from the maternal burrow 26 days after their mother was first seen with enlarged mammae indicating that parturition occurred approximately a month previously. Most young were born around the third week of April in 1972 and 1973. Trapping was avoided during this period. Parturient or close to parturition female thirteen-lined ground squirrels change burrows or move their litter if captured at that time (McCarley, 1966).

Richardson′s ground squirrels are not commonly observed to breed above ground (Quanstrom, 1968), and no copulation was ever observed during this study. A few females captured in early April had swollen vulvae but no accurate determination of the mean date of breeding was obtained from the small number observed. Denniston (1957) estimated gestation to be 17 days, based on an observed copulation of a captured female and her subsequent parturition. Asdell (1964), based on Howell′s (1938) findings for captive

Table 2. Calendar of the observed annual cycle of Richardson's ground squirrel in the Youngstown area for 1972 and 1973.

	1972			1973		
MEAN DATE OF:	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
Juvenile emergence	May 14 (M.8-22) *10	May 25 (M.18-J.5) *10	May 25 (M.18-J.2) *2	May 15 (M.11-20) *9	May 20 (M.16-21) *3	May 21 (M.21) *2
Onset of hibernation for: adult males	June 11 (J.6-15) *5	June 21 (J.19-26) *3	June 12 (J.7-19) *3		June 8 (J.4-20) *4	June 4 (J.4) *2
adult females: - breeding	June 15 (J.7-19) *7	July 2 (J.19-Ju.28) *10	June 18 *3	June 19 (M.25-Ju.19) *9	June 10 (J.4-20) *6	June 16 (J.9-23) *4
- non-breeding		June 9 (J.6-19) *8	June 8 (J.2-14) *6	June 4 (M.14-J.23) *12	June 3 (M.30-J.8) *6	June 4 (M.30-J.9) *2
juveniles: - females #	July 23 (Ju.14-28) *12	Aug. 4 (Aug.4-6) *4	Aug. 1 (Ju.28-A.4) *2	-	-	-
- males	-	-	-	-	-	-

*: sample size (number of litters for juvenile emergence, or number of squirrels for onset of hibernation); #: these figures are the earliest that juvenile females were thought to go into hibernation; many juvenile females and males were still active above ground when field work was terminated each year (Sept. 12, 1972; Aug. 28, 1973); ( ): earliest and latest dates observed; - : juveniles are still active when observations were stopped in late August.

squirrels, estimated gestation to be 28 to 32 days. Nellis (1969) and Sheppard (1972), taking Asdell (1964) as their source, used a 28-day gestation period. Michener (1977) estimated the gestation period to be 24 days; her estimate seems to be the most accurate since it was based both on field and laboratory observations. If breeding occurred 24 days prior to parturition, it must follow that on average, breeding occurred around March 27 in 1972 and March 24 in 1973.

By the time field work commenced around the middle of March each year, a few squirrels had already emerged from hibernation, and by the end of March most were active above ground. All were trapped and marked by the first week of April. Breeding occurs within one or two weeks after emergence from hibernation (Yeaton, 1972; Dorrance, 1974), or based on observed dates of emergence and subsequent parturition, only 2 days after emergence (Michener, 1977). Mean dates of emergence can thus be approximated as being March 11-25 in 1972, and March 8-22 in 1973.

In 1972 and 1973, juveniles emerged significantly earlier on plot 1 than on plot 2 (Mann-Whitney, S.95) and plot 3 (Mann-Whitney, S.95), while there was no significant difference between the two latter plots (Mann-Whitney, N.S.). In the Richardson′s ground squirrel, date of breeding was shown to be related to body weight; heavy females breed earlier than smaller females (Dorrance, 1974). Such seems to be the case here as well. In April each year, adult females from plot 1 were significantly heavier (16-18%) than females from plot 2 (t-test, S.99.9) and plot 3 (t-test, S.99.9); these two latter groups did not differ significantly in weight (t-test, N.S.) (App. 8A).

B. Onset of hibernation

Adults and juveniles, males and females, do not go into hibernation at the same time. Observation of individual adult males above ground ceased on the average dates of June 14, 1972 (n=11) and June 7, 1973 (n=6). Similarly, non-breeding adult females disappeared around June 10 (n=14) and June 4 (n=20) in 1972 and 1973, preceding the males by a few days (Table 2). Breeding females, i.e. those observed lactating or seen with juveniles, remained above ground as late as June 28, 1972 (n=20) and June 16, 1973 (n=19). These figures are the mean of all individual observations for each plot as presented in Table 2. It is noticeable that in 1973, each group of adults went into hibernation sooner than it did in 1972 (t-test, S.95).

What could be the onset of hibernation for juvenile females was observed in 1972. In each plot, juvenile females 'disappeared' from the plots where they had well-established homes between July 14 and August 6 (Table 2). At that time, populations were stable; all juvenile males and the few remaining juvenile females were still active and had established home burrows when field work was terminated on August 12, 1972. The fact that many of these juvenile females were trapped the following spring indicates that either they had dispersed nearby and came back to the plots in the spring, or most likely, they had hibernated early within the plots themselves. Dorrance (1974) observed that in central Alberta, juvenile females immerge in late August and early September, while juvenile males hibernate after September 1. In 1973, all juveniles established in the plots were still active on August 28 at which time field work was terminated. Nine males and 6 females were then present on plot 1. In the Youngstwon area, juveniles are still active above ground well into September and even into October, at which time however, the population is composed mostly of juvenile males (Mohl, 1974). Thus in 1972 and 1973, the onset of hibernation occurred in the following chronological order: 1. non-breeding adult females, 2. adult males, 3. adult breeding females, 4. juvenile females, 5. juvenile males.

It is worthwhile to quantify the annual span of active time spent by each class of squirrel between emergence and onset of hibernation. This period can be compared with the metabolic requirements of each class. For example, a breeding female has higher metabolic demands than a male or a non-breeding female (Sadleir, 1969); similarly an adult squirrel needs less time to accumulate reserves necessary for hibernation than a juvenile squirrel that must also undergo body growth. No individual dates of adult emergence are known since many squirrels had already emerged when field work started in March; however, trapping records indicated that all adults had emerged by April 1. The active time span spent above ground by individual adult squirrels between April 1 and the last date they were observed may be an adequate measurement of the time necessary for each class of adult squirrel to prepare for hibernation. Similarly, this period of time for juveniles is the time elapsed between their birth and the last date they were seen above ground. The date of birth is obtained by subtracting 30 days from observed dates of emergence of juveniles. So for all adult and juvenile squirrels for which these dates were observed, the span of time spent between emergence or birth and last appearance above ground were calculated and are presented in Table 3.

The order in which squirrels went into hibernation (Table 2) was the same as the ranking of the number of days they were active between April 1 or birth and onset of hibernation (Table 3); the squirrels active for the least number of days went into hibernation first. However, statistical analysis shows that there is no significant difference between the active periods spent by adult males and non-breeding adult females (t-test, N.S.). Clark (1970), Yeaton (1972) and Dorrance (1974) observed that adult males emerged at least one or two weeks before adult females; this was not taken into account in using April 1 as the initial date of activity above ground. This could mean that non-breeding females do in fact spend less time above ground than adult males. Breeding females spend a longer time above ground (between 12 to 18 days) than both adult males (t-test, S.99) and non-breeding adult females (t-test, S.99.9) (Table 3). This was also observed by Michener (1978). Finally, juveniles spend more time above ground than any other age class (Table 3).

A relationship seems to exist here between the periods of activity spent above ground by different groups of squirrels and their respective metabolic requirements. This is especially obvious within the groups of adult squirrels. In effect, the adults with the least energy demands, i.e. treated non-breeding females and adult males, were the first to return into hibernation, while breeding females were the last to do so. Such a phenomenon should be illustrated by weight differences in these groups of squirrels. Repeated weighing of individuals from early April 1972 until their return into hibernation revealed that during the period April to May 1972, breeding females increased their body weight by 12% while adult males and non-breeding adult females showed significantly higher increases of 28% (Chi-square, S.95) and 40% (Chi-square, S.99.9) (App. 8B). There was no significant difference in the weight increases of treated and non-treated

Table 3. Estimates of mean numbers of active days for adult squirrels between first observation and return into hibernation, and for juveniles between birth and onset of hibernation, in plots 1, 2 and 3 during the summers 1972 and 1973.

	1972	1973	1972-1973
NON-BREEDING ADULT FEMALES	71± 5 (14)	65± 13 (20)	67± 11 (34)
ADULT MALES	75± 6 (11)	68± 6 (6)	72± 7 (17)
BREEDING ADULT FEMALES	89± 13 (20)	77± 15 (19)	82± 15 (39)
JUVENILE FEMALES	101± 13 * (18)	a minimum of 131 days (12)**	
JUVENILE MALES	a minimum of 113 days (31)**	a minimum of 131 days (14)**	

( ) : sample size; * : minimum figure since not all juvenile females had gone into hibernation when field work was terminated; ** : these juveniles were still active when observations were ceased on August 12, 1972 and August 28, 1973. These are the minimum number of days between their presumed date of birth and cessation of observations.

males (Chi-square, N.S.), or between males and non-breeding adult females (Chi-square, N.S.). A significant linear correlation exists between body weight and lipid levels in the Richardson's ground squirrel (Zegers et al., 1977) and it was shown that onset of hibernation is partly determined by initial body weight and by the rate of weight increase (Tubbs, 1977; Michener, 1978). This seems to be the case here as well.

Adult males, non-breeding and breeding females were active for averages of 75, 71 and 89 days during the 1972 season (Table 3), which gives an average of 80±12 (S.D.) days (n=45). In 1973, the same groups of adult squirrels respectively spent 68, 65 and 77 days above ground (Table 3), for an average of 70±14 (S.D.) days (n=45). For each group of squirrels, and for all squirrels combined, the average period of activity was significantly shorter in 1973 than in 1972 (t-test, S.99.9).

Since no accurate dates were obtained for the individual time of squirrel emergence, it is not known if such a difference is significant. However, I believe that the shorter activity period observed in 1973 was due to changes in weather. Thus a short summary of pertinent climatic conditions will be given below. Factors of predation will also be considered.

C. Weather and predation

In 1972 and 1973, monthly temperatures (as recorded by a government weather station 35 miles distant) averaged 50°F during the months of March to June. During the same months, total precipitation was 6.53 inches in 1972 and 9.42 inches in 1973 (Alberta Environment, 1972 and 1973). However weather can vary within only a few miles on the prairies, and it was my impression that more rain fell in the Youngstown area in 1973. This impression was corroborated by Mr. J. Schmidt, a farmer living 4 miles north of my study area who kept a record of rainfall. Mr. Schmidt informed me that from his measurements that year, 13 to 15 inches of rain had fallen between spring thaw and August 7, 1973. From his records, 4 inches had fallen during the same period in 1972. I recorded the occurrence of rain during the study period and noted that in 1972, rain fell on 26% of the days when observations were made, whereas in 1973 it rained on 33% of the observation days (from App. 2).

Spring was colder in 1974 than it was in 1972 and 1973. Between October 1973 and May 1974, 8.06 inches of rain/snow fell whereas only 5.34 inches fell during the same period in 1972-1973 (Alberta Environment, 1972, 1973 and 1974). Moreover, average temperature from January to the end of April 1974 was colder (9.7°F) than during the same months in 1973 (18°F).

Vegetation growth was not quantified but I noticed that in 1973, as a result of the extra rain, vegetation of the surrounding area was much greener than that observed in 1972. Two figures are presented here to illustrate this phenomenon. Figure 2A shows plot 1 and was taken on July 1, 1972; Figure 2B shows this same plot and was taken on July 10, 1973. Vegetation was green on both years but it can be seen quite readily that vegetation was much taller and lusher in 1973.

A better condition of the vegetation, and thus of the food supply for herbivores, is usually reflected in the animal populations. Seventy-three percent of the Richardson's ground squirrel diet is composed of green plants (Clark, 1970), thus a change in vegetation is likely to influence its population. Such changes were observed in rodent populations inhabiting desert environment (Whitford, 1976) as most resident species, one of them a ground squirrel, responded to fluctuations in rainfall. Droughts brought reductions in density, whereas favourable rainfall and vegetation production were characterized by population recoveries. In populations of round-tailed ground squirrels studied in Arizona, data accumulated during a 16-year period showed that litter size (measured by the number of embryos) was correlated to rainfall, as the latter affected the production of spring annuals on which the squirrels feed (Reynolds and Turkowski, 1972). In central Alberta, Dorrance (1974) could not show a direct relationship between populations of Richardson's ground squirrel and the biomass of the vegetation present. On the other hand, he established a correlation between the biomass of vegetation and female weight. Since heavier females have a larger number of embryos (Dorrance, 1974), it is likely that in this species also, and in vegetation conditions more similar to those observed in my study area, food supply i.e. vegetation as affected by rainfall, should be reflected in the squirrel populations. Such was the case as will be shown in the population dynamics section.

Figure 2A. Vegetation on plot 1; July 1, 1972

Figure 2B. Vegetation on plot 1; July 10, 1973

The better conditions found in 1973 can also have an impact on the predator populations. It was shown by Pitelka et al. (1955) that the numbers and reproduction of snowy owls and other lemming-eating predators vary greatly between years according to the number of lemmings available. The number of predators was observed each year during a specifically measured period of time. This and other observations made during 1972 and 1973 are used to demonstrate different predatory pressure that may have been experienced by the squirrel populations.

More predators were observed per observation period on the plots in 1973 than in 1972. Averages of 0.19 hawks, 0.01 weasels and 0.01 badgers were observed for each 45-minute observation period in 1972; averages of 0.35 hawks, 0.04 weasels and 0.06 badgers were seen during 1973 (Table 4). These species are known predators of the Richardson's ground squirrel. In central Alberta, 32% of the total biomass of prey taken by red-tailed hawk is composed of this ground squirrel species (Luttich et al., 1970), and the long-tailed weasel can be an important predator, taking juveniles weighing up to 400 grams (Dorrance, 1974). Hawks and badgers are considered to be main predators in Saskatchewan (Michener, 1968). Forty-one percent of 92 terrestrial predator feces contained Richardson's ground squirrel remains in a study made by Sheppard and Swanson (1976).

Overall, 0.22 such predators were observed in an average observation period in 1972, while twice as many (0.45) were observed in 1973 (Table 4; Chi-square, S.99.9). Moreover, only one weasel was removed in plot 1-1972 in order to protect the ground squirrels whereas 15 weasels were removed from this same plot during the same period in 1973. Control of predators such as weasels was more thorough on the control plot (#1) than it was on the other two plots. Plot 1 was only a few hundred feet from the trailer where I was living in the field. Thus the presence of any predator was detected much more easily, particularly during the day. By contrast, oppurtunities to observe predators on plots 2 and 3 were less, as predators were seen only during the hours of the day that were used to make behavioral observations or to trap the squirrels in these plots.

As a result of more rain in 1973 than in 1972, vegetation was much lusher in 1973. Predators were more numerous, and as will be shown in the population dynamics section, generally more juvenile ground squirrels were

Table 4. Estimation of predator abundance on plots 1, 2 and 3 during observation periods in 1972 and 1973.

	1972				1973			
PLOTS	1	2	3	ALL PLOTS	1	2	3	ALL PLOTS
NUMBERS OF ANIMALS SEEN								
hawks [1]	7	13	10	30	10	11	6	27
weasels [2]	2	0	0	2	3	0	0	3
badgers [3]	3	0	0	3	2	2	1	5
Total	12	13	10	35	15	13	7	35
NUMBER OF OBSERVATION PERIODS	54	51	50	156	36	21	21	78
NUMBER OF ANIMALS PER OBSERVATION PERIOD								
hawks	0.13	0.25	0.20	0.19	0.28	0.52	0.29	0.35
weasels	0.04	0.0	0.0	0.01	0.08	0.0	0.0	0.04
badgers	0.06	0.0	0.0	0.01	0.06	0.10	0.05	0.06
Total	0.22	0.25	0.20	0.22	0.42	0.62	0.33	0.45

1. *Buteo swainsonii*, *B. regalis*, 2. *Mustela frenata longicauda*, 3. *Taxidea taxus*

born in 1973. Also, I believe that the better vegetation observed in 1973 may have contributed to the shorter activity period of the adult ground squirrels that year, as observed between April 1 and their individual return into hibernation.

D. Summary

In the Youngstown area, observations in this study and findings of other researchers indicated that most ground squirrels emerge during the latter part of March and that by the beginning of April, most have bred. Parturition occurred around the third week of April and juveniles emerged from early May until early June, with peak of emergence occurring around the third week of May.

Onset of hibernation followed a chronological order that was a function of the age, sex and reproductive condition of individual squirrels. Non-breeding females, mostly mestranol treated females, were the first to return to hibernation in early June, followed closely by adult males. Breeding females spent significantly more time above ground and on the average did not return into hibernation until late in June. Juveniles were still active after September 12 but there was evidence that some juvenile females entered hibernation in August. All squirrels, adult or juveniles, remain for many months in hibernation and do not emerge until the following March. The annual cycle is illustrated in Figure 3.

The time spent between emergence or birth and onset of hibernation seemed related to the different metabolic demands made on different categories of squirrels. Squirrels that had greater metabolic demands, such as breeding females, spent more time above ground. The period of adult activity between emergence and return into hibernation was also affected by the vegetation conditions of the area. In 1973, more rain resulted in a lusher vegetation and in an earlier return into hibernation for adult squirrels. Squirrel predators were more abundant in 1973.

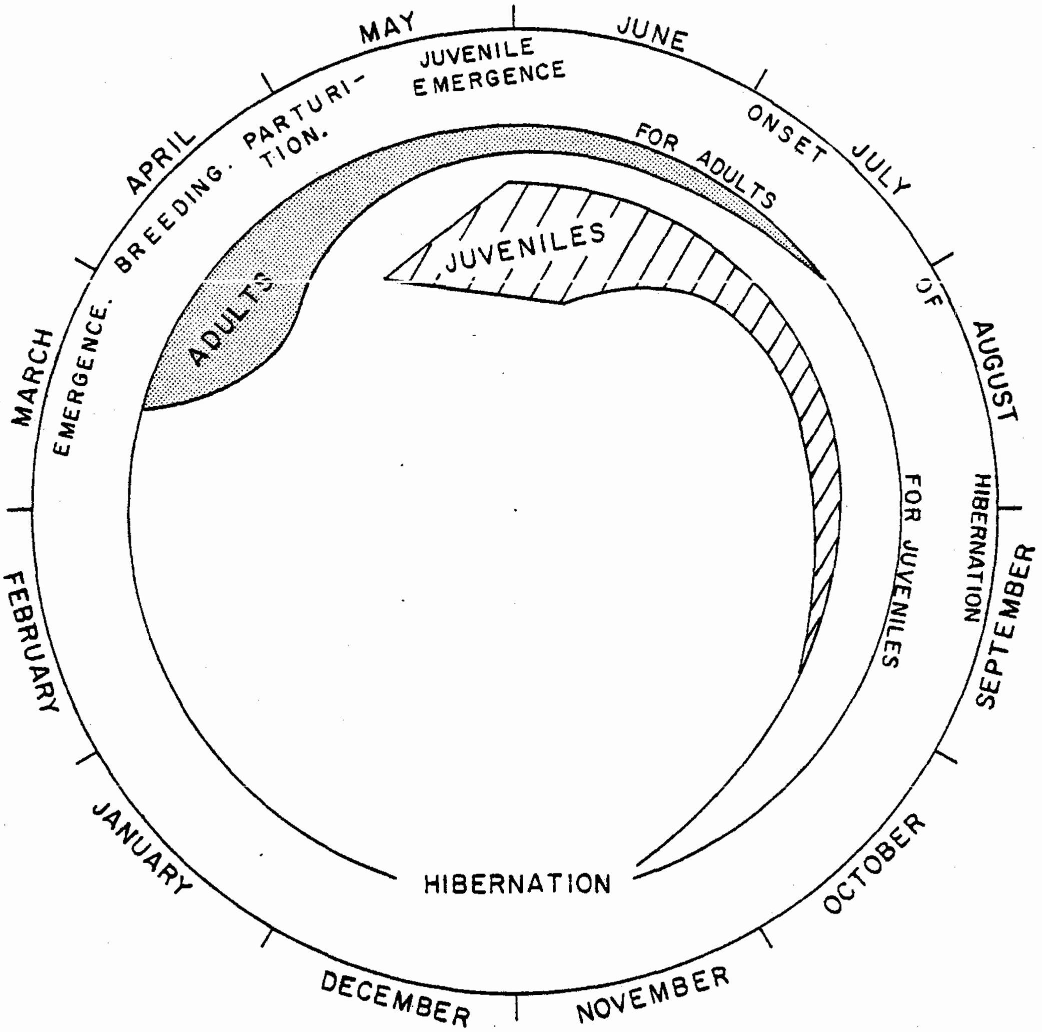


Figure 3. Annual cycle of the Richardson's ground squirrel in the Youngstown area, Alberta. Relative changes in numbers is indicated by the width of the marked blocks.

RESULTS PART III. POPULATION DYNAMICS

A. Introduction

The population numbers of a colony are altered by natality and mortality, and by ingress and egress. In Richardson's ground squirrel, such movements seem to be closely related to the social behavior of the squirrels inhabiting the colony. Adult males are the first squirrels to emerge in spring and their home ranges encompass many female burrows (Yeaton, 1972). After breeding, females establish territories (Yeaton, 1972) and many squirrels are expelled from the colony. Resident males are excluded from most females' territories by mid-April (Yeaton, 1972). The adult population remains more or less stable in numbers from this time until adult males and females return into hibernation. The numbers in the colony are maintained by juveniles emerging from the maternal burrows during May and June. However, only a few of these are left with home burrows at the end of the summer and a few, mostly females, hibernate within the home area (Michener and Michener, 1973).

B. Population 1972

1. Adult population: April 1972

a. Densities

In April 1972, the three 4-hectare plot areas surrounding plots 1, 2 and 3 (Fig. 1) were intensively live-trapped to yield respectively 42, 41 and 36 squirrels; all three areas had roughly equivalent populations, i.e. 10, 10 and 9 squirrels per hectare (Table 5). However, the squirrels were not uniformly distributed within each 4-hectare area so that densities were different within the boundaries of plots 1, 2 and 3. Twenty-four squirrels were trapped in plot 1, while 20 and 10 were captured in plots 2 and 3 (Table 5; Fig. 4). The corresponding densities were of 37, 29 and 12 squirrels per hectare in plots 1, 2 and 3 respectively (Table 5). As plots 1 and 2 had much higher densities than their surrounding 4-hectare plots 1A and 2A, it seems that these plots were more 'desirable' habitats for the ground squirrels than plot 3. In this latter plot, density was more

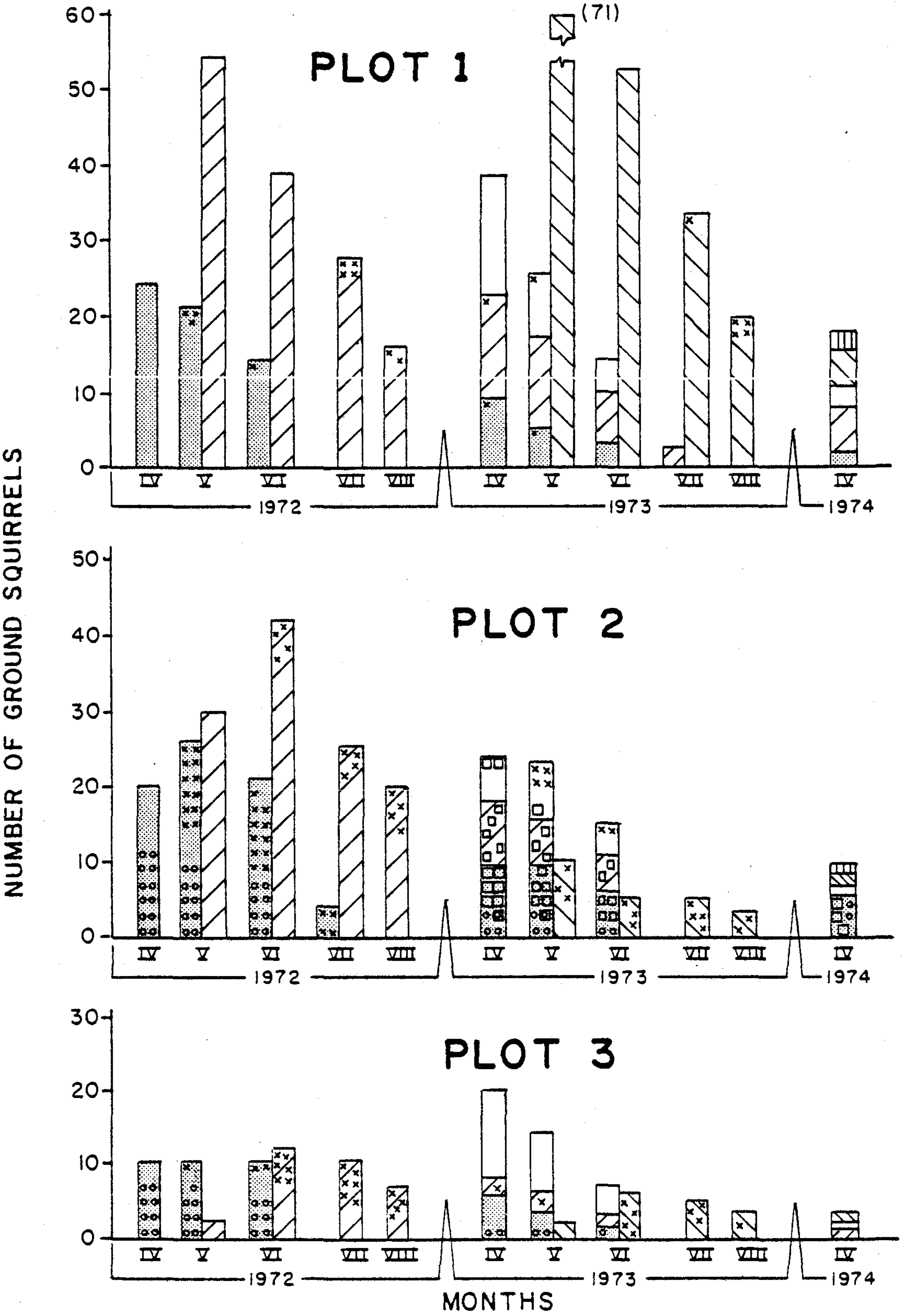
Table 5. Numbers, densities and sex ratio of adult ground squirrels present on plots 1A, 2A, 3A, 1, 2 and 3 between April 1972 and April 1974.

TIME OF OBSERVATION AND PLOTS TRAPPED	NUMBERS OBSERVED			DENSITY squirrels/hectare			SEX RATIO number of females/male		
	PLOTS #1	#2	#3	PLOTS #1	#2	#3	PLOTS #1	#2	#3
APRIL 1972									
Plots 1A, 2A, 3A	42	41	36	10.4	10.1	8.9	2.0	4.1	2.0
Plots 1, 2, 3	24	20	10	36.9	29.0	12.3	3.0	3.0	9.0
MAY 1972. Plots 1,2,3									
total population	21	26	10	32.3	37.7	12.3	2.0	3.3	9.0
resident population	10	21	10	15.4	30.4	12.3	4.0	6.0	9.0
APRIL 1973									
Plots 1, 2, 3	37	24	20	56.9	34.8	24.7	11.3	2.0	2.3
MAY 1973. Plots 1,2,3									
total population	26	23	14	40.0	33.3	17.3	25.0	2.8	3.7
resident population	14	16	10	21.6	23.2	12.3	No male	4.3	4.0
APRIL 1974									
Plots 1, 2, 3	16	9	3	27.7	13.0	3.7	5.0	8.0	No male

Figure 4. Numbers of Richardson's ground squirrels present in plots 1, 2 and 3 between April 1972 and 1974

▒	adult squirrels initially trapped in 1972
□	adult squirrels initially trapped in 1973
▥	adult squirrels initially trapped in 1974
▨	juvenile squirrels initially trapped in 1972
▧	juvenile squirrels initially trapped in 1973
○	number of circles denotes the number of squirrels in each category which were treated with mestranol in April 1972
□	number of squares denotes the number of squirrels in each category which were treated with mestranol in April 1973
×	number of crosses denotes the number of squirrels which moved into the plots between April and September each year

IV: April V: May VI: June VII: July VIII: August


NUMBER OF GROUND SQUIRRELS
PLOT 1
(71)
60
50
40
30
20
10
0
IV
V
VI
VII
VIII
1972
1973
1974
PLOT 2
50
40
30
20
10
0
PLOT 3
30
20
10
0
MONTHS

comparable to that of the 4-hectare area surrounding it, (12 versus 9) (Table 5).

b. Sex ratio. Age distribution.

The sex ratio in April showed a dominance of females, especially in plot 3 where only one male was trapped with 9 females; in plots 1 and 2, three females were found for every male (Table 5). The proportions of males in the three populations did not differ significantly as males represented 25%, 25% and 10% of the April populations in plots 1, 2 and 3 respectively (Chi-square, N.S.). Such disproportionate sex ratio in favour of adult females are common in populations of Richardson's ground squirrels (Nellis, 1969; Yeaton, 1969; D.R. Michener, 1972; Sheppard, 1972; Dorrance, 1974).

All squirrels trapped in April 1972 were classified as 'adults' although it is very likely that some of them were yearlings; their age class was given as "1 year +" since they had at least undergone one season of hibernation.

c. Mestranol treatment

In plot 2, 8 of the 15 females captured previously within the plot boundaries were recaptured on April 10 for mestranol treatment; four of the 5 males present at that time were also treated (Table 6, A). In plot 3, I attempted on April 12 to recapture the 9 females present; however only 7 were treated since two females avoided recapture until early May at which time it was judged to be too late for treatment as they were already lactating. No squirrel was treated in plot 1 (Table 6,A).

2. Adult population: May 1972

During May, squirrels consistently occupied a given area within the plots and were agonistic to neighbours and trespassers if these came close to their home burrow. Those squirrels still retaining a home burrow within the plot boundaries by the end of May or having bred in the plot (females only) were considered as "residents". Some of the trespassers were squirrels previously trapped within the plot boundaries in early April that did not succeed in maintaining a home burrow on the plot; some had a home area adjacent to the plot and were seen quite frequently in the plots. Other trespassers were never trapped until May and therefore must have come from outside the 4-hectare areas trapped in early April (it is assumed that

Table 6. Numbers of adult ground squirrels trapped and observed within the boundaries of plots 1, 2 and 3 during the field seasons 1972 and 1973.

	1972						1973					
	PLOT 1		PLOT 2		PLOT 3		PLOT 1		PLOT 2		PLOT 3	
A. Trapped in April	18f	6m	15f	5m	9f	1m	34f	3m	16f	8m	14f	6m
A1. treated	-	-	8	4	7	1	-	-	9	4	-	-
B. Present in May	14f	7m	20f	6m	9f	1m	25f	1m	17f	6m	11f	3m
B1. trapped in April	14	4	10	4	9	0	24	1	14	4	11	3
B11. treated	-	-	8	2	7		-	-	8	2	-	-
B111. residents	-	-	8	1	7		-	-	7	1	-	-
B12. non-treated	14	4	2	2	2		24	1	6	1	11	3
B121. residents	8	2	2	0	2		14	0	6	1	8	2
B2. moved in since April	0f	3m	10f	2m	0f	1m	1f	-	3f	2m	-	-
B21. residents		0	8	2		1	0	-	0	1	-	-
B3. all residents in May	8f	2m	18f	3m	9f	1m	14f	0m	13f	3m	8f	2m
Immigration between April and May (B21/(A+B2)) x 100	0% (0/27)		31% (10/32)		9% (1/11)		0%		3% (1/29)		0%	
Emigration/mortality between April and May ((A-B1)/(A+B2))x100	22% (6/27)		19% (6/32)		9% (1/11)		32% (12/38)		21% (6/29)		30% (6/20)	
% of April population (A) remaining as resident in May ((B111+B121)/A) X 100	42% (10/24)		55% (11/20)		90% (9/10)		38% (14/37)		62% (15/24)		50%(65)* (10/20)	
%of May population (B) that is resident (B3/B) x 100	48% (10/21)		81% (21/26)		100% (10/10)		54% (14/26)		70% (16/23)		71%(93)* (10/14)	
% of April-May (A+B2) resident in May (B3/(A+B2)) x 100	37% (10/27)		66% (21/32)		91% (10/11)		37% (14/38)		55% (16/29)		50%(65)* (10/20)	

f : female; m : male; ( ) : numbers used to calulate percentage; ( )* : percentage obtained when three resident squirrels killed by a badger in late April are taken into consideration.

all squirrels present in the 4-hectare areas were trapped in April). They were present quite often in the plots during certain periods and accounted for many interactions with the resident squirrels; they were designated as squirrels trying to "move in". Some of these succeeded in establishing home burrows within the plot boundaries and were considered as "immigrants". Finally transient squirrels were observed only once or twice going through the plots; most were never captured and they are not considered in the study of populations dynamics.

The establishment of home areas resulted in considerable changes in the populations over the summer. These changes will be described here and related to the different mestranol treatements given to the populations.

a. Densities

When compared to the April population, total numbers of squirrels trapped or observed in May within the plots' boundaries had decreased in plot 1 (-13%), increased in plot 2 (+30%), and remained the same in plot 3 (Table 6; Fig. 4). These changes were due to immigration and emigration and/or mortality, because by May all squirrels had emerged from hibernation and none had returned (Fig. 3).

Six squirrels disappeared between April and May on both plots 1 and 2, reducing the total populations on these plots by 22% and 19% respectively. Similarly one male squirrel disappeared from plot 3, so that emigration/mortality accounted for 9% of the losses from this plot (Table 6). There was no significant difference in emigration between any of the three plots (Chi-square, N.S.), although more squirrels moved out or died on the high density plots i.e. 1 and 2.

Immigration did not occur to all plots. One male squirrel moved onto plot 3, replacing the one that disappeared, thus leaving the population unchanged (Table 6). Three squirrels moved onto plot 1 while as many as 12 did so on plot 2 (Table 6, B2); however while none succeeded in establishing a home burrow in plot 1, as many as 10 remained as residents in plot 2 (Table 6, B21). Correspondingly, immigration represented 0%, 31% and 9% of the total populations trapped on plots 1, 2 and 3 respectively (Table 6). Immigration onto plot 3 did not differ significantly from that observed in plots 1 (Chi-square, N.S.) and 2 (Chi-square, N.S.), while plot 2 had significantly more immigrants than plot 1 (Chi-square, S.99.9). The lack of difference observed between plots 2 and 3 was probably due to the small number of squirrels involved in plot 3, i.e. only 1 immigrant squirrel.

b. Residency

The proportion of squirrels that established themselves as resident was larger in the treated plots and may be related to the mestranol treatment. Forty-two percent, 55% and 90% of the squirrels first trapped in plots 1, 2 and 3 in early April remained resident in May (Table 6). Significantly more of them remained on plot 3 than on the control plot 1 (Chi-square,S.95). Plots 1 and 2 did not differ significantly (Chi-square, N.S.) and there was no significant difference between the two treated plots (Chi-square, N.S.). This seems to indicate that lower population density and desirability on plot 3 was more significant than the mestranol effects in affecting the squirrels′ success to establish residency.

Proportionally more of the squirrels which moved in during May or late April established residency in the treated plots than in the non-treated one. While none of the 3 squirrels attempting to move onto plot 1 succeeded, 83% (10 out of 12) and 100% (1 out of 1) of the immigrating squirrels became resident on plots 2 and 3 (Table 6). There was a significant difference between the control plot and plot 2 (Chi-square,S.99.9), while the small number of squirrels concerned in plot 3 did not allow detection of any significant difference between this plot and plots 1 and 2.

Overall, 66% and 91% of all squirrels were resident on plots 2 and 3, while only 37% were resident on the control plot (Table 6). The control plot differed significantly from plot 2 (Chi-square, S.99) and from plot 3 (Chi-square,S.99.9). There was no difference between the most treated plot (#3) and the least treated one (#2).

c. Mestranol treatment and its effect on residency status

In plot 2, 10 of the 12 squirrels (83%) treated in early April were still present in May and 9 of these (75%) were residents; in contrast, only 4 of the 8 non-treated squirrels (50%) captured in early April survived to May and only two of these (25%) were residents (Table 6). Not only were there more treated than non-treated squirrels left in May (Chi-square, S.95), but also proportionally more of them were residents (Chi-square, S.99.9). Comparisons were made on plot 2 as it was only on this plot that the environmental conditions were the same for sizable groups of treated and non-treated squirrels; vegetation or other factors could be different in other plots and affect survival. As such, comparisons between treated squirrels from one plot, and non-treated squirrels from another were precluded. Any difference observed on plot 2 between treated and non-treated squirrels was likely to be a result of the mestranol treatment.

In plot 2, the lower rate of residency of non-treated squirrels as compared to treated squirrels, was compensated by many non-treated squirrels moving into the plot and establishing home burrows. As a result, the May resident population was composed of 9 treated squirrels and 12 non-treated ones (Table 6). In total, 9 of the treated squirrels became residents (75%); 12 of the 20 non-treated squirrels (60%) present in April and moving in later also became residents (Table 6). When these immigrant non-treated squirrels are taken into account, no significant difference can be shown between treated versus non-treated squirrels in regard to establishing residency.

In plot 2, treated squirrels were more successful in establishing residency between April and May than the original cohort of non-treated squirrels. Thus during April, the proportion of treated squirrels in the population increased as more of the non-treated animals disappeared from the plot. However, in late April, immigrants (and therefore non-treated individuals) moved into the plot, so that the proportion of resident treated squirrels in the population declined and again was comparable to that of non-treated

d. Sex ratio

Sex ratio changed slightly between April and May as core areas were established. As populations were increased or reduced, different proportions of males and females moved in or out. In May, 2.0, 3.3 and 9.0 females were present for every male on plots 1, 2 and 3. Resident population sex ratios were more favorable to females generally being of 4.0, 6.0 and 9.0 females for every male in plots 1, 2 and 3 respectively (Table 5). Of the populations present then, proportionally more females than males established residency, at least in plots 1 and 2; however, chi-square comparisons between the total population and the May resident population sex ratio failed to show any significant differences. Moreover, the sex ratio in May was the same as it was in April, although females may have been more successful than males in establishing residency. In fact, it was observed by Dorrance (1974), that in populations of Richardson's ground squirrels, sex ratio is more unbalanced in May than in April, and this in favor of females.

3. Adult population: June-July 1972

Onset of hibernation in 1972 was first observed on plot 3 (June 11, n=12), then on plot 1 (June 13, n=12) and last on plot 2 (June 22, n=21) (Table 2). Mann-Whitney ranking tests showed that treated females (June 10, n=11) and adult males (June 14, n=11) went into hibernation earlier than non-treated females (June 28, n=20). Adult males from plot 2 hibernated later (June 21, n=3) than males from plot 1 (June 11, n=5; Mann-Whitney, S.95) and plot 3 (June 12, n=3). Similarly, non-treated females from plot 2 (July 2, n=10) hibernated later than non-treated females from plot 1 (June 15, n=7; Mann-Whitney, S.99.9) and plot 3 (June 18, n=3; Mann-Whitney, S. 95). This late onset of hibernation on plot 2 may be related to the fact that plot 2 has a much denser resident population than plots 1 and 3 (Table 5) in 1972. The social "stress" induced by higher squirrel numbers may possibly delay fat accumulation on onset of hibernation.

4. Juvenile population 1972

Most litters observed in 1972 emerged from the maternal burrow during the latter part of May (Table 2). Juvenile emergence was well synchronized inside each plot. All juveniles emerged within approximately a two-week period on all plots: plot 1 (May 8-22), plot 2 (May 18-June 5) and plot 3 (May 18-June 2)(Table 2). However, the average date of emergence was earlier on plot 1 (May 14, n=10) as litters emerged about 11 days before litters from plot 2 (May 25, n=10) and plot 3 (May 25, n=2) (Mann-Whitney, S.99) As a result of these emergence patterns, the numbers of juveniles present on the three plots at one time were not comparable. Thus their numbers are best compared in relation to the number of weeks elapsed since the mean juvenile emergence date for each given plot.

a. Natality

The eight resident females in plot 1 all reproduced and 55 juveniles were observed emerging at their burrows (Table 7). That all females should reproduce seems normal in populations of Richardson's ground squirrels. D.R. Michener (1972), Sheppard (1972) and Dorrance (1974) reported that from 92% to 100% of all female ground squirrels were lactating in their study populations.

In plot 2, none of the eight mestranol treated females resident in May gave birth; the remaining 10 non-treated females, also resident in this plot, all reproduced and 41 juveniles were captured at their home burrows (Table 7). In plot 3, 9 females were resident in May of which 7 were treated; one of the latter was seen with a single young, while the 2 non-treated females produced 5 more juveniles (Table 7). Sex ratio of new born was roughly 1:1 on all plots (Table 7, B).

It is obvious that as more females were treated in a given plot, fewer juveniles were born since fewer resident females bore litters. The effect was directly related to the degree of mestranol treatment, being greatest on plot 3 (Table 7, D). A further reduction in the number of juveniles born was due to the smaller emerging litter size on the treated plots (Table 7, C). In plot 3, litter size was biased as the litter of a single juvenile produced by a treated female was taken into account; still the 2 non-treated females were seen with only 5 juveniles, resulting in an average litter size of 2.5 emerging juveniles per parturient female. The fact that females from plots 2 and 3 had smaller litters than females from plot 1 may depend on females from these plots having lighter body weights than females from plot 1 (App. 8A), rather than being a result of the mestranol treatment. In some species, smaller females give birth to smaller litters, which is possibly related to the reduced availability of uterine space (Sadleir, 1969, p.202).

The reproductive output of the treated plots was thus greatly reduced. The numbers of juveniles born on plots 2 and 3 were only 1/3 and 1/10 of that observed on the control plot (Table 7, D), when all resident females are taken into account.

Table 7. Recruitment of juveniles onto plots 1, 2 and 3 through natality and immigration.

	1972			1973		
Plot #	1	2	3	1	2	3
A. Total number of resident females	8	18	9	14	13	8
A1. treated with mestranol	0	8	7	0	7	0
A2. observed with young	8	10	3*	14	3	2
A3. non-treated, not seen with young	0	0	0	0	3	6
B. Number of emerging young	28F 27M	22F 19M	3F 3M	38F 33M	3F 3M	1F 1M
C. Litter size	6.9	4.1	2.0	5.1	2.0	1.0
D. Number of young per resident female	6.9	2.4	0.7	5.1	0.1	0.3
E. Number of young per hectare	84.6	59.4	7.4	109.2	8.7	2.5
Number of immigrating juveniles	1F 3M	2F 2M	3F 3M	2F 2M	3F 1M	2F 2M
Total number of juveniles trapped within the plot boundaries during the summer (May-Sept.)	29F 30M	24F 21M	6F 6M	40F 35M	6F 4M	3F 3M

*: one of these females was treated with mestranol in early April

b. Population fluctuations

The number of juveniles present in a given plot was initially a result of natality. The maximum number of young born on each plot was observed about a week after first juvenile emergence. After that time, juvenile populations declined steadily as a result of dispersal and/or mortality. This decline was somewhat compensated for by the immigration of juveniles from outside the plots.

Mortality and emigration cannot be distinguished from one another in this study. Some juveniles were observed as far as half a mile from their home burrows. Others were found dead within the plot boundaries, killed by a badger or a hawk. Also a number of very young juveniles, which hadn't emerged from the maternal burrow, were thought to have died as a result of torrential rain in early June 1973. It is not known what proportion of juveniles died or just moved out. Mortality and emigration will be treated as one here, and any reference to "emigration" will automatically mean "and/or mortality".

Many foreign juveniles moved into the plots and were observed to interact with resident squirrels. Only those establishing home burrows within the plot boundaries are considered as immigrants. Juveniles born from resident females are designated as "born juveniles".

Densities of 85, 59 and 7 juveniles per hectare were born on plots 1, 2 and 3 respectively (Table 7). From their maximum numbers of 55, 41 and 6 born juveniles, born populations dropped steadily. Juvenile immigration alleviated the decline in plot 1 and 2, and actually increased the juvenile population present in plot 3 (Fig. 5; Fig. 6).

Decline of born juvenile populations followed the same pattern in all plots (Fig. 6). The biggest drop in numbers occurred during the first four weeks following emergence. There was no difference in survival patterns between plots 1 and 2. Survival on plot 3 was higher (50%) than on plot 1 (21%; Chi-square, S.99.5) and on plot 2 (29%; Chi-square, S.97.5) (Fig. 6). No relationship could be shown between born juveniles' emigration and/or mortality and the mestranol treatment, but the lowest dispersal was seen on the least dense plot. Plots 1 and 2, having higher densities, had a higher juvenile dispersal.

Figure 5. Numbers of juvenile squirrels born on the plots and of immigrant juveniles on plots 1, 2 and 3 in 1972 and 1973.

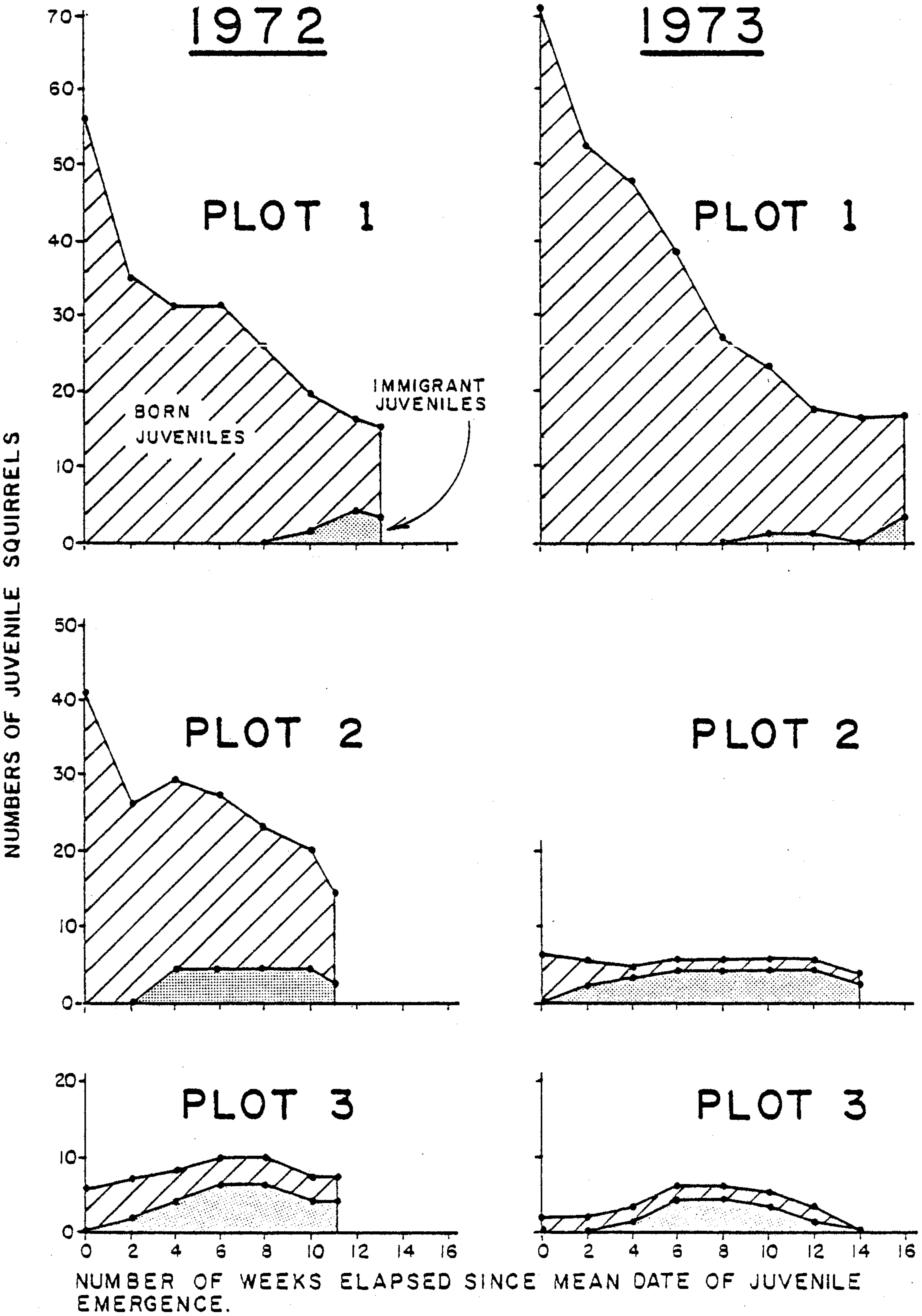
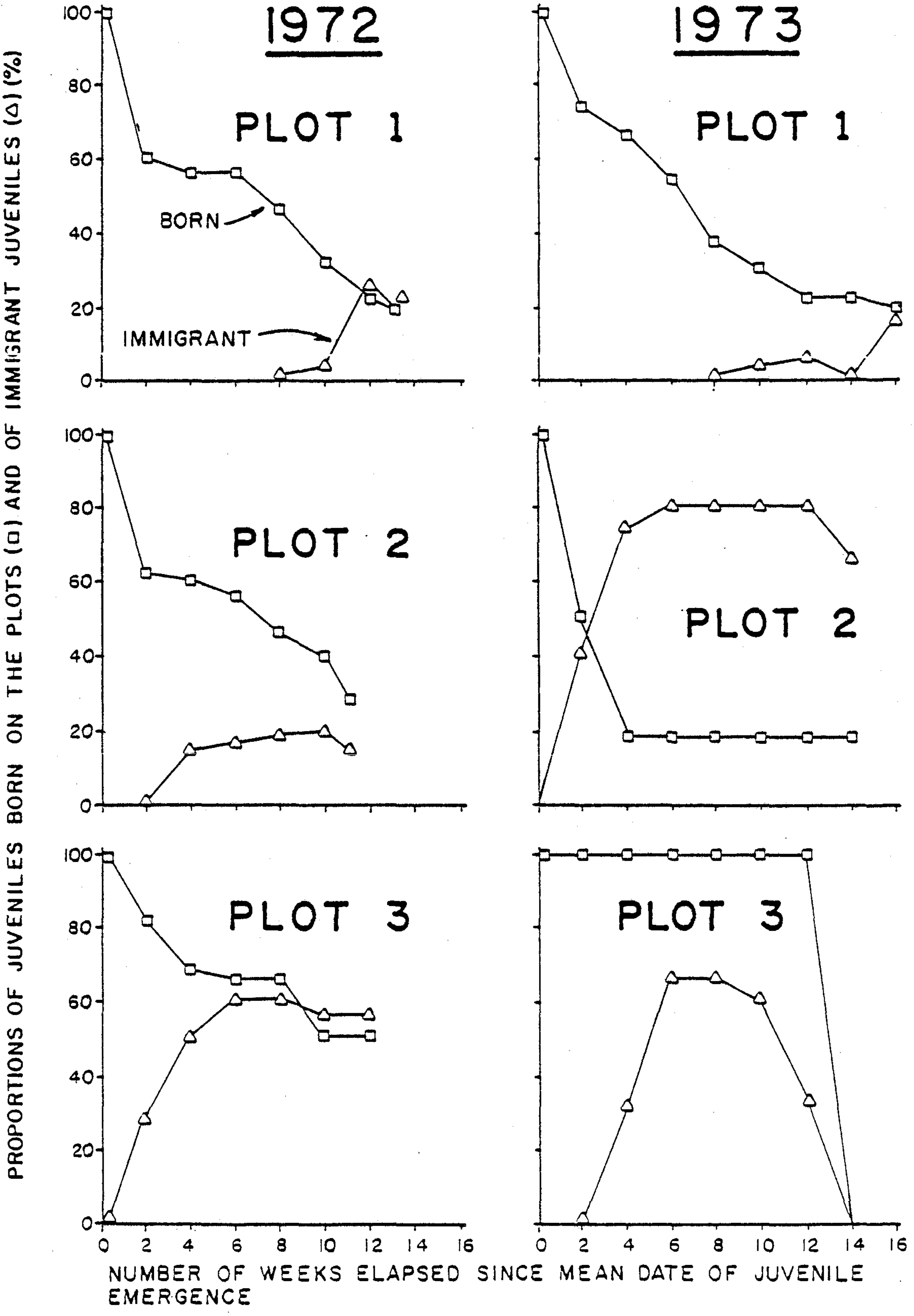

1972
1973
PLOT 1
PLOT 1
BORN JUVENILES
IMMIGRANT JUVENILES
PLOT 2
PLOT 2
PLOT 3
PLOT 3
NUMBERS OF JUVENILE SQUIRRELS
0
10
20
30
40
50
60
70
0
10
20
30
40
50
0
10
20
0 2 4 6 8 10 12 14 16
0 2 4 6 8 10 12 14 16
NUMBER OF WEEKS ELAPSED SINCE MEAN DATE OF JUVENILE EMERGENCE.

Figure 6. Proportions of juvenile squirrels born on the plots and of immigrant juveniles on plots 1, 2 and 3 in 1972 and 1973.


1972
1973
PLOT 1
PLOT 2
PLOT 3
BORN
IMMIGRANT
PROPORTIONS OF JUVENILES BORN ON THE PLOTS (□) AND OF IMMIGRANT JUVENILES (△) (%)
0
20
40
60
80
100
0
2
4
6
8
10
12
14
16
NUMBER OF WEEKS ELAPSED SINCE MEAN DATE OF JUVENILE EMERGENCE

The onset of juvenile immigration occurred much earlier on the treated plots than on the control plot. Juvenile immigrants moved into plots 2 and 3 only 4 and 2 weeks after mean juvenile emergence, while they were not observed until 10 weeks after such emergence in plot 1 (Fig. 5).

The numbers of juvenile immigrants were roughly the same in all plots, (i.e. 4, 4 and 6), but the proportions of the total juvenile populations they represented on each plot were quite different (Fig. 6). Of totals of 59, 45 and 12 individual juveniles trapped on plots 1, 2 and 3 during the summer 1972, 7%, 9% and 60% were immigrants (from Table 7). There were proportionally more immigrants on plot 3 than on plot 1 (Chi-square, S.99.9) and plot 2 (Chi-square, S.99). The two latter plots did not differ significantly (Chi-square, N.S.).

However some difference in juvenile immigration was shown between plot 1 and plot 2 when numbers of juveniles present at a given time were considered. For example, 4 weeks after their respective mean dates of emergence, a greater portion of the plot 2 juvenile population (17%) was composed of immigrants as compared to that observed on plot 1 (0%) (Chi-square, S.97.5). This situation remained unchanged after 8 weeks (17% versus 0%; Chi-square, S.97.5). However after 12 weeks on plot 1, and after 11 weeks on plots 2 and 3, 25%, 14% and 57% of the juvenile populations were composed of immigrants (Fig. 6). At that time, juvenile females and especially those in plot 1 (Table 2) were already going into hibernation. Immigration increased on plot 1, and at that time, plot 3 had a greater proportion of immigrants than the control plot (Chi-square, S.99). Overall, juveniles immigrated quite freely into the treated plots during the whole summer while on the control plot, they did so only at the end of the summer when hibernation of juveniles had started.

The cohorts of born juveniles decreased steadily on all plots, but to a lesser degree on plot 3, the least dense plot. Immigration compensated for reduced natality on plots 2 and 3 as juveniles immigrated earlier onto these treated plots and formed larger proportions of the juvenile populations.

5. Summary : adult and juvenile populations 1972

ADULT POPULATION

April 1972

1. Squirrel density averaged 37 and 29 squirrels per hectare on plots 1 and 2 and only 10 on plot 3. Thus plots 1 and 2 were more productive or desirable than plot 3.
2. Sex ratio was the same on all plots and all squirrels were considered as adults.
3. No squirrel was treated with mestranol on plot 1, while 60% and 80% of the April female populations were treated on plots 2 and 3.

May 1972

4. Numbers of squirrels were changed on the plots partly as a result of differential immigration. The population of the control plot (#1) was reduced by 13%, while 30% more squirrels were found on plot 2. Numbers did not change on plot 3.
5. Emigration could not be shown to differ significantly between the plots, but more immigration occurred onto plot 2 than onto plot 1, though both had a similar density of squirrels in April. Less immigration occurred onto plot 3 than onto plot 2.
6. Establishment of the home burrows also affected the May populations. Success of residency establishment was different on the three plots. Squirrels from a low density, treated plot (#3) were more successful in maintaining themselves as residents than squirrels from higher density plots, treated (#2), or not treated (#1).
7. Immigrant squirrels were more successful in establishing residency in treated plots (#2,3) than in non-treated plots (#1).
8. When all squirrels trapped in April, plus those immigrating during April and May were considered, larger numbers of squirrels established themselves as residents on treated plots than on the non-treated plot.
9. The establishment of home burrows in the plots seems to have generally favoured females in most plots but no statistical differences could be shown between males and females. As a result, the sex ratio in May was the same as in April and did not differ between the treated plots and the control plot.

10. Mestranol treated squirrels were more successful in maintaining themselves as residents than non-treated squirrels from the same plot (#2). However, their advantage was eliminated as non-treated squirrels immigrated onto the treated plots and successfully established residency.

June 1972

11. Squirrels from all plots were hibernating or preparing to do so. Mestranol treated females did not breed and hibernated earlier than breeding females.
12. Population density affected squirrels and the onset of hibernation. A high population density apparently inhibited the accumulation of fat and thus delayed onset of hibernation. As a result, breeding females and adult males from plot 2, the plot with the highest resident density, hibernated later than their counterparts from plots 1 and 3.
13. Heavier squirrels went into hibernation earlier than light body weight squirrels on plots of equal densities.

JUVENILE POPULATION

14. Natality was drastically reduced on the treated plots as 44% and 78% of the resident females were sterilized and did not produce young. Only 2.4 and 0.7 juveniles were produced for each resident female in these plots, as opposed to a higher number of 6.9 juveniles in the control plot.
15. Natality was also reduced on the treated plots because litter size was smaller on these plots. Females from plots 2 (4.1 young per reproducing female) and 3 (2.0) had smaller litter sizes than females from the control plot (6.9). Females from plots 2 and 3 also had smaller body weights. The fact that the smallest litter size was observed on plot 3, the most treated plot, may reflect poorer environmental conditions rather than an effect of the mestranol treatment.
16. Juveniles emerged earlier on plot 1 than on plots 2 and 3. This seems to be related to the fact that breeding females on plot 1 were heavier than females from plots 2 and 3.
17. Populations of born juveniles declined similarly on all plots, but proportionally reached lower levels on plots 1 and 2 than on plot 3.

This is possibly a result of the higher juvenile densities observed on plots 1 and 2.

18. Immigration occurred sooner on the treated plots, and immigrants represented a larger portion of the juvenile populations on these plots as compared to the control plot. This was especially so on plot 3, the most treated and least dense plot.

C. Population 1973

1. Adult population: April 1973

a. Densities

In April 1973, 37, 24 and 20 squirrels were trapped on plots 1, 2 and 3, resulting in densities of 57, 35 and 25 squirrels per hectare on these plots (Table 5). There were increased numbers on all plots compared to April 1972. In effect, 1.5, 1.2 and 2 times more squirrels were trapped on plots 1, 2 and 3 respectively in April 1973 than in April 1972 (from Fig. 4).

These changes in population densities to April 1973 seem to be inversely related to the resident population densities observed on the plots in 1972. The least increase was seen on plot 2, a plot where resident density in 1972 was greatly increased as a result of the mestranol treatment. The largest increase was seen on plot 3, the least dense plot in 1972. While not differing significantly from the increase observed on the control plot (#1), the increase on plot 3 was significantly greater than observed on plot 2 (Chi-square, S.99.9).

b. Sex ratio

The control plot (#1) had a significantly smaller proportion of adult males than plot 2 (Chi-square, S.99.9) and plot 3 (Chi-square, S.99.5) in April 1973. The sex ratio had been the same on all plots in April 1972 (Section III.B.2.b).

Proportionally more females per male (11 to 1) were trapped on plot 1-1973 than in 1972 (3 to 1)(Table 5; Chi-square, S.95). This change was due to an increase of the number of females and to a decrease of the number of males on plot 1 (Table 6). In contrast, more males were found on plots 2 and 3 in April 1973 than in 1972 (Table 6). The largest increase occurred on plot 3, the most extensively treated plot in 1972 (Table 1). When compared to 1972, the proportion of males was significantly increased on plot 3-1973 (Chi-square, S.99), while it remained the same in plot 2 (Chi-square, N.S.).

The changes in sex ratio between April 1972 and April 1973 were thus related to the mestranol treatment given in April 1972. The non-treated plot had a significant decrease in its male population, whereas a 50%

treated plot kept the same sex ratio, and an 80% treated plot had a significant increase in the proportion of males. The more intensive the treatment in 1972, the larger the proportion of males resulted. If this relationship is of any significance, it indicates that adult males had better chances of maintaining themselves around treated plots as opposed to non-treated plots.

c. Mestranol treatment and breeding status

No treatment was given to animals on plot 1-1973 and this plot again acted as the control plot. In plot 2-1973, 13 squirrels present in April were treated, one of them having been already treated in April 1972 (Fig. 4; Table 6). Two of the females treated in April 1972 were present in April 1973 but were not re-treated. A total of twenty-four squirrels were present on plot 2 in April 1973 (Table 6) and fifteen of them were affected by mestranol in either 1972 or 1973. No squirrels were treated in plot 3-1973 (Table 1), and only two females treated in April 1972 were present in April 1973 (Fig. 4).

d. Age distribution and population composition

In April 1973, the populations found on plots 1, 2 and 3 were composed of three groups of squirrels: 1. adults trapped in 1972 which survived the winter, 2. juveniles born in 1972, now yearlings, which over-wintered, and 3. new squirrels not previously trapped, which were designated as adults of unknown age (Table 8). These three groups of squirrels were present in different proportions on the three plots. Proportionally more survivors, yearlings (2) and adults(1), were found on plot 1 - 62% (Chi-square, S.95) and plot 2 - 74% (Chi-square, S.99.9) than on plot 3 - 40% (Table 9). As a result, the group of new squirrels (3) was greater on plot 3 (60%) than on plot 1 (38%) (Chi-square, S.95). On plot 2, 25% of the April squirrels were new arrivals but their proportion was not significantly less than on plot 3 (Table 9; Chi-square, N.S.).

The lower number of survivors on plot 3-1973 could have resulted from a differential annual survival. Annual survival was calculated for each group of squirrels. Comparisons were made between plots and between groups to determine the role of factors such as treatment, residency, sex, and plot on annual survival.

Table 8. Age distribution of the adult and juvenile populations present on plots 1, 2 and 3 during 1972, 1973 and 1974.

COHORTS OF SQUIRRELS (Age class no.) AND TIME OF OBSERVATION	NUMBERS OF SQUIRRELS TRAPPED								
	PLOT 1			PLOT 2			PLOT 3		
	Female	Male	total	Female	Male	total	Female	Male	total
1972 POPULATION Apr.-Sept.									
1. adults first trapped in 1972 (age unknown, 1 year+)	18	9	27	25	7	32	9	2	11
2. juveniles born in 1972	29	30	59	24	21	45	6	6	12
1973 POPULATION Apr.-Sept.									
1. adults first trapped in 1972 (2 years+)	7	2	9	9	0	9	4	1	5
2. juveniles born in 1972 (1 year)	14	0	14	5	4	9	3	0	3
3. adults first trapped in 1973 (age unknown, 1 year+)	13	1	14	2	4	6	7	5	12
4. juveniles born in 1973	40	35	75	6	4	10	3	3	6
1974 POPULATION April									
1. adults first trapped in 1972 (3 years+)	2	0	2	5	0	5	0	0	0
2. adults, born in 1972 (2 years)	6	0	6	0	0	0	1	0	1
3. adults first trapped in 1973 (2 years+)	3	0	3	1	0	1	1	0	1
4. juveniles born in 1973 (1 year)	3	1	4	2	0	2	1	0	1
5. adults first trapped in 1974 (age unknown, 1 year+)	1	2	3	-	1	1	-	-	-

- : indicates the absence or the impossibility for a given group of squirrels to be present in a given plot at that time. By contrast, '0' indicates that it was possible for squirrels belonging to a given group to be present, but that none were trapped or observed then.

Table 9. Proportions of the 1972, 1973 and 1974 April populations represented by adult and juvenile survivors and by new adult squirrels (not previously trapped) on plots 1, 2 and 3.

COHORTS OF SQUIRRELS (Age class no.) TRAPPED IN APRIL EACH YEAR	PERCENTAGE OF THE APRIL POPULATION REPRESENTED BY A GIVEN COHORT		
	PLOT 1	PLOT 2	PLOT 3
APRIL 1972			
1a. adults first trapped in Apr. 1972 (age unknown, 1 year+)	100% (24)	100% (20)	100% (10)
APRIL 1973			
1. adults first trapped in 1972 (2 years+)	24% (9)	37% (9)	25% (5)
2. juveniles born in 1972 (1 year)	38% (14)	37% (9)	15% (3)
3a. adults first trapped in Apr. 1973 (age unknown, 1 year+)	38% (14)	25% (6)	60% (12)
APRIL 1974			
1., 2. and 3. adults surviving from 1972 and 1973 (2, 2+, 3+ years)	61% (11)	67% (6)	67% (2)
4. juveniles born in 1973 (1 year)	22% (4)	22% (2)	33% (1)
5a. adults first trapped in Apr. 1974 (age unknown, 1 year+)	17% (3)	11% (3)	0% (0)

( ) : numbers of squirrels belonging to a given age class (from Table 9).

The annual survival rates of all adult and juvenile squirrels were 0.27, 0.25 and 0.35 on plots 1, 2 and 3 respectively (from Table 10); no statistical differences were found by chi-square tests. No difference could be shown in the survival of adults and juveniles when comparisons were made for each group between the plots. Overall, adult and juvenile survival were the same on the treated plots as on the control plot during the 1972-1973 winter.

Treated squirrels from plots 2 and 3 had a combined survival rate of 0.35, while non-treated squirrels, which did not differ significantly, had a survival of 0.32 (Table 10; Chi-square, N.S.). When plots were considered individually however, treated females (0.62) on plot 2 survived significantly better than non-treated ones (0.23) (Table 10; Chi-square, S.97.5). On plot 3, no difference could be shown between these two groups.

Resident (i.e. those squirrels having a home burrow within the plots′ boundaries) and non-resident (i.e. those squirrels trapped within the plots in April 1972 and 1973, but which did not have a home burrow within the plots boundaries) squirrels showed similar survival rates on all plots (Chi-square tests). When plot data were combined, no differences could be shown between resident (0.37) and non-resident (0.27) survival (Table 10).

When all plots were considered, adults survived better (0.33) than juveniles (0.23)(Table 10; Chi-square, S.95), although this difference could not be shown in any individual plot.

Females survived better than males in both adult and juvenile age classes of all plots combined. Adult females had a survival rate of 0.38 while adult males averaged only 0.17 (Chi-square, S.99.9). Statistical differences between the survival of adult males and females could not be shown in the separate plots. Juvenile females had a better survival (0.39) than juvenile males (0.07) when all plots were taken into consideration (Chi-square; S.99.9). A difference was shown between plots 1 and 3, where juvenile females had survival rates of 0.48 and 0.50 compared with rates of 0 (Chi-square, S.99.9) and 0 (Chi-square, S.95) for juvenile males (see materials and methods section for Chi-square test procedure when value equals zero). In plot 2, no difference could be shown between the survival of male (0.19) and female (0.25) juveniles (Chi-square, N.S.). It is possible that the survival of juvenile males was better on the treated plots

Table 10. Annual survival of adult and juvenile ground squirrels initially trapped during the 1972 season (April-September) on plots 1, 2 and 3, and still present on these plots in April 1973.

COHORTS OF SQUIRRELS AND 1972 STATUS	SURVIVAL number of squirrels belonging to a given 1972 cohort and surviving to April 1973, divided by the total number of squirrels belonging to that same cohort in 1972											
	PLOT 1			PLOT 2			PLOT 3			ALL PLOTS		
	Female	Male	total	Female	Male	total	Female	Male	total	Female	Male	total
ADULTS, first trapped in 1972, 1	0.39 (18)	0.22 (9)	0.33 (27)	0.36 (25)	0 (7)	0.28 (32)	0.44 (9)	0.50 (2)	0.45 (11)	0.38 (52)	0.17 (18)	0.33 (70)
a.1. residents * in 1972	0.37 (8)	0.50 (2)	0.40 (10)	0.35 (17)	0 (3)	0.30 (20)	0.44 (9)	1.0 (1)	0.50 (10)	0.38 (34)	0.33 (6)	0.37 (40)
a.2. non-residents in 1972 *	0.40 (10)	0.14 (7)	0.29 (17)	0.37 (8)	0 (4)	0.25 (12)	-	0 (1)	0 (1)	0.39 (18)	0.08 (12)	0.27 (30)
b.1. treated in 1972	-	-	-	0.62 (8)	0 (4)	0.42 (12)	0.29 (7)	0 (1)	0.25 (8)	0.47 (15)	0 (5)	0.35 (20)
b.2. non-treated in 1972	0.39 (18)	0.22 (9)	0.33 (27)	0.23 (17)	0 (3)	0.20 (20)	1.0 (2)	1.0 (1)	1.0 (3)	0.35 (37)	0.23 (13)	0.32 (50)
JUVENILES born in 1972, 2 (now yearlings)	0.48 (29)	0 (30)	0.24 (59)	0.25 (24)	0.19 (21)	0.22 (45)	0.50 (6)	0 (6)	0.25 (12)	0.39 (59)	0.07 (57)	0.23 (116)

1,2 : age classes as given in Table 8, ( ) : number of squirrels belonging to a given cohort in 1972. * : from Table 6, N.B. : survival calculation : in Table 8, it is shown that 18 adult females were present on plot 1-1972; 7 of them survived to April 1973, thus a survival of 7/18 = 0.39.

than on the control. On plot 2, a sufficient number of juvenile males in 1972 survived to 1973 and demonstrated the advantage resulting from the mestranol treatment, since juvenile males on that plot (0.19) survived better than juvenile males on the control plot (0)(Chi-square, S.97.5). The number of juveniles on plot 3-1972 was always very low (Table 7 or Fig. 4) so that juvenile males were not present in sufficient numbers to show any effect of the 1972 mestranol treatment.

2. Adult population: May 1973

a. Densities

When compared to April 1973 populations, the total numbers of adults in May had decreased by a third on plots 1 and 3, the non-treated plots, and did not alter on plot 2, a 50% treated plot (Table 6; Fig. 4). The reductions in numbers on plots 1 (Chi-square, S.99.5) and 3 (Chi-square, S.99.9) between April and May were significantly greater than had been observed on the same plots between April and May in 1972 (Table 6). This may have resulted from the higher densities of squirrels observed on these plots in April 1973. In plot 1-1973, 56.9 squirrels per hectare were present in April, as opposed to only 36.9 in 1972 (Table 5). Similarly in plot 3, 24.7 squirrels per hectare were present in 1973 versus 12.3 in 1972. However, plot 2-1973 (34.8 squirrels per hectare) also had a higher density than plot 2-1972 (29). The difference between the plots is thus again attributed to the treatment. Squirrel population decreased on non-treated plots, while it did not on a treated plot.

Plot 2-1973 differed from plot 2-1972 in regards to immigration. The increase in population that characterized plot 2 between April and May 1972 did not occur in 1973 (Table 6). There was effectively no immigration onto the plots in early 1973. Little immigration had occurred into plot 1 and plot 3 in 1972. However, immigration into plot 2 was significantly higher in 1972; 31% of the April-May 1972 population was composed of immigrants compared to 3% in 1973 (Table 6; Chi-square, S.99.5).

Immigration and/or mortality was similar on all plots in 1973 as 32%, 21% and 30% of the April-May populations of plots 1, 2 and 3 were lost. However, when losses were compared for a given plot between 1972 and 1973, differences emerged. Losses from plots 1 and 2 were the same in 1972 and

1973 (Chi-square, N.S.), whereas it was significantly greater on plot 3-1973 than it was in 1972. Thirty percent and 9% of the April populations had disappeared from plot 3 by May in 1973 and 1972 respectively (Table 6; Chi-square, S.99.5). The decrease in adult population could partly result from increased predation pressure (Table 4). At least two resident females and one male were killed by a badger between April 22 and 25 on plot 3; no predation was observed in 1972.

Overall, in 1973, as a result of immigration, emigration and mortality, populations on the non-treated plots (#1, #3) were reduced by a third between April and May, while the number of squirrels remained the same on the treated plot (#2). Resulting population densities of 40.0, 33.3 and 17.3 resident adults per hectare were observed on plots 1, 2 and 3 during the month of May 1973 (Table 5).

b. Residency

The proportions of squirrels in the populations that established themselves as residents in 1973 were approximately the same on all plots (Table 6; Chi-square, N.S.). This lack of difference occurred despite the fact that squirrels on plot 2 surviving from April 1973 were more successful in maintaining themselves on this plot than squirrels from the control plot. Sixty-two percent of the April population on plot 2 was still resident in May compared to 38% of the population on plot 1 (Table 6; Chi-square, S.97.5). A high survival and residency rate was also observed on plot 2 in 1972, probably an effect of mestranol treatment. The residency rate of plot 3, a treated plot in 1972, was higher than the control plot in 1972. In 1973, plot 3 was not treated and its residency success was the same (50%) as observed in the control plot (37%) (Table 6; Chi-square, N.S.). However, 3 squirrels considered as residents were killed by a badger at the end of April 1973 on plot 3. If these squirrels were counted as residents, 65% of the plot 3-1973 would have been resident (Table 6). This was significantly greater than what was observed on the control plot (37%) (Chi-square, S.97.5), but did not differ from plot 2. It is thus possible that population density, as well as treatment, may affect the squirrels residency. Squirrels from treated or low density plots may be more successful in establishing residency than squirrels from high density or non-treated plots.

Success in establishing residency was compared between years for each plot. The proportions of the population which established territories on plot 1 were the same in 1972 and 1973 (37%) despite an increased overall density in April 1973 (Table 5). The same occurred in plot 2, i.e. 66% in 1972 and 55% in 1973 (Chi-square, N.S.). On plot 3, a lower proportion were residents in 1973 than in 1972, i.e. 50% in 1973 and 91% in 1972 (Table 6; Chi-square, S.99.9). Note that plot 3 was not treated in 1973, in contrast to 1972 (Table 1).

Although the proportion of squirrels which established residency was similar in the two years on plot 1, the total number present in April 1973 (37) was greater than in April 1972 (24) so that the number of residents was greater in 1973 (14 vs. 10) (Table 6). On plot 2, the proportion of squirrels establishing residency was not significantly different between 1972 and 1973, and the same number of squirrels (26) were available in May each year (Table 6). However the large immigration observed in 1972 did not take place in plot 2-1973 and the number of residents in May was reduced, i.e. 16 residents in 1973 versus 21 in 1972 (Table 6). The proportion of squirrels remaining as residents on plot 3 was less in 1973 than in 1972. However, initial numbers of squirrels was greater in April 1973 than in April 1972, i.e. 20 squirrels versus 10 (Table 6). As a result, as many squirrels (10) were left as resident on plot 3-1973 as on plot 3-1972 (Table 6) for a resident density of 12.3 squirrels per hectare (Table 5). If the 3 resident squirrels that were killed by a badger at the end of April were taken into consideration, plot 3 would have had more residents in 1973 (13) than in 1972 (10) (Table 6).

In 1973, plots 1 and 2 had the same resident densities which were both higher than that observed on plot 3. This relationship between plots was similar to the one observed in 1972. But the situation had changed within some of the plots. When compared to 1972 populations, resident densities had increased on plot 1, decreased on plot 2 and remained the same on plot 3 during May 1973 (Table 5).

c. Mestranol treatment and its influence on residency status

On plot 2-1973, thirteen squirrels were treated in April 1973 and one male and seven females remained as residents in May 1973 (Table 6). Two females treated in April 1972 survived to April 1973 and became residents in

May 1973 (Fig. 4). Three of the females present in April 1973 and not treated then were given mestranol in May 1973 when lactating. Overall, 12 of the 13 resident females (92%) and one of the three resident males on plot 2-1973 were treated in 1973 or in 1972. This situation is very similar to the one observed on plot 3 in 1972, when 7 of the 9 resident females, i.e. 78% were treated (Table 6). Details on the outcome of breeding for all females will be given in the juvenile population section when discussing natality in 1973.

In 1972, treated squirrels were more successful than non-treated squirrels in establishing residency (Section III.B.2.c). However in 1973, the group of non-treated squirrels present in plot 2 was so small, that a difference between the treated and non-treated squirrels could not be shown. Of a total of 15 squirrels treated in April 1972 or 1973, 11 (73%) established residency in 1973; eight squirrels, non-treated in April 1972 or 1973, were present in April 1973 and 4 (50%) were left as residents in May 1973. No significant difference could be shown between the two groups' residency success rate (Chi-square, N.S.).

d. Sex ratio

In May 1973, sex ratio among the resident populations was of 4.3 (n=16) and 3.7 (n=10) females for every male on plots 2 and 3 respectively and no male was resident on the control plot (Table 5). No significant difference in sex ratio could be shown between the plots (Chi-square tests). Between April and May 1973, the number of males was reduced on all plots as home areas were established. Three, 8 and 6 males were seen on plots 1, 2 and 3 during April 1973; 0, 3 and 2 males were left in May 1973 (Table 5). Thus the difference in sex ratio that existed between the control plot and plots 2 and 3 in April 1973 had disappeared by May 1973 after home burrows were established.

3. Adult population: June-July 1973

By June of 1973, few adult squirrels were left on the three plots (Fig. 4). Adult squirrels had already started going into hibernation and many had succumbed to predators. All adult squirrels had gone into hibernation by July 19 (Table 2).

The average dates of entry into hibernation were similar on all plots in 1973: June 10 (n=22) on plot 1, June 8 (n=17) on plot 2 and June 10 (n=8) on plot 3 (from Table 2). Treated females (65 days between April 1 and hibernation) spent less time above ground than breeding females (77) (Table 3; t-test, S.95). Unlike 1972, males did not differ significantly from either group in 1973 (Section I.B).

In 1973, although non-breeding females still went into hibernation earlier than breeding females, the difference in time was less. In 1972, non-breeding females went 18 days before breeding females; in 1973, this difference in timing was 12 days (from Table 3). The overall return into hibernation occurred earlier in 1973 than in 1972 (Section I.B). These differences were observed for all categories of squirrels, but the effect was especially marked in breeding females (Table 3).

Body weight affected the onset of hibernation in 1972 with heavier animals going into hibernation first (Section I.B). In 1973, the average body weight of squirrels on plot 2 (296.6 g, n=29) (t-test, S.99.9) and on plot 3 (282.7 g, n=26) (t-test, S.99.9) was significantly lighter than for animals on plot 1 (334.9 g, n=39) (App. 8B). Thus it would have been expected that squirrels from plots 2 and 3 would have gone into hibernation later than squirrels from plot 1. However the majority of squirrels on plots 2 and 3 did not breed in 1973 (Table 7), and were thus able to accumulate fat at a faster rate than heavier but breeding squirrels from the control plot. This compensated for their smaller initial body weight, and as a result, time of immergence was the same on all plots.

4. Juvenile population 1973

In 1973, most litters emerged from the maternal burrow during the last half of May, averaging May 15 (n=9) on the control plot (#1), May 20 (n=3) on plot 2 and May 21 (n=2) on plot 3 (Table 2). As in 1972, juveniles from the control plot emerged sooner than on plot 2 (Mann-Whitney, S.97.5) or plot 3 (Mann-Whitney, S.99). The numbers of juveniles will therefore be compared on the basis of weeks elapsed since mean date of emergence on each plot, rather than to the actual date.

a. Natality

The 14 resident females from plot 1 all gave birth (Table 7), but one of them, though she was seen to be lactating, was never observed with young. Her offspring possibly drowned during a torrential storm at the end of May. Seventy-one juveniles were trapped on plot 1, giving an average of 5.1 juveniles per parturient and resident female (Table 7).

On plot 2, six of the females present in May were not treated with mestranol in April 1973; but, two of these were treated in April 1972, and three of the four remaining were given mestranol when lactating in May 1973. Only one of the females treated in 1972 was seen with juveniles (2) although both females were lactating. One of the females treated in May was seen with a single young, and the one female that was never treated had a litter of three. Seven females that had been treated with mestranol in April 1973 were resident in May; none of them was seen with young. Reduced natality on plot 2-1973 can thus be partly attributed to the mestranol treatments given to animals on this plot. However, only 6 juveniles were born in plot 2 (Table 7), although six of the females reproduced. I believe that the treatment given in May to lactating females, as well as the increased number of predators and torrential rain observed in 1973 were responsible for the death in-burrow of most of the juveniles born to these breeding females.

On plot 3, 8 females were resident in May 1973 (Table 6); none had been treated in April 1973, but two had been in April 1972 (Fig. 4). Both of the latter females were lactating in May of 1973 but only one was seen with a single young (App. 7). Of the six females remaining and never treated with mestranol, three were either pregnant or lactating when trapped in May, but only one had a single young above ground. Thus on plot 3, only two young were born to 8 resident females (Table 7). This low natality cannot be attributed to mestranol treatment or to an absence of males as six adult males were present in April 1973 (Table 6). I think that many litters were born in the burrows on plot 3 but these disappeared as a result of bad climatic conditions and increased predation (Table 4). Torrential rain fell on May 19 (App. 2), before litters emerged on plot 3 (Table 2). Most litters on plot 1 had already emerged (Table 2).

In 1973, more young were born on the control plot than in 1972. This was due to the presence of more resident breeding females as litter size was slightly reduced (5.1 young per female in 1973 versus 6.9 in 1972)(Table 7). On plot 2, natality was greatly reduced when compared to 1972. Most females were sterilized by mestranol, and those that bred had smaller litters (2.0) in 1973 than in 1972 (4.1) (Table 7). In plot 3, only two young were observed although 8 females could have potentially bred on that plot. This low number of born juveniles was thought to result primarily from rainfall and increased predation.

b. Population fluctuations

The numbers of juveniles initially observed on the three plots in 1973 resulted from natality, i.e. juveniles born within the plots' boundaries. During the summer, the numbers of juveniles born on the plots steadily declined, and immigrant juveniles born elsewhere moved in.

In 1973, the decline of the juvenile population on plot 1 followed the same pattern noted in 1972. Four, 8 and 12 weeks after mean juvenile emergence, respectively 66%, 38% and 23% of the born juveniles were left; in this plot in 1972, 56% (Chi-square, N.S.), 47% (Chi-square, N.S.) and 22% (Chi-square, N.S.) were left after the same period (Fig. 6). These percentages did not differ significantly from those observed in 1973, in spite of the fact that many more juveniles were born on the plot in 1973.

The decline of the born juvenile population on plot 2 was very different from that seen on the control plot, and was also different from the decline observed in plot 2 in 1972. On plot 2 in 1972, 61%, 46% and 29% of the born juveniles were left after 4, 8 and 12 weeks (Fig. 6) which did not differ significantly from the 1972 decline on the control plot. In 1973 in contrast, 4 weeks after mean juvenile emergence, there were only 17% of the born juveniles left on plot 2, a proportion which differs significantly from the 66% of born juveniles left on plot 1 (Chi-square, S.95). After 8 weeks, 17% of the born squirrels were still left in plot 2, which by then did not differ significantly from the 38% of born juveniles observed in the control plot (Fig. 6; Chi-square, N.S.). From then on, plot 2 did not differ from plot 1 and at the end of the summer, i.e. 14 weeks after mean juvenile emergence in each plot, roughly the same proportions of born juveniles were left, i.e. 23% in plot 1, and 17% in plot 2 (Fig. 6;

Chi-square, N.S.). Overall, plot 2 differed from the control plot in 1973 in that the decline of born juveniles was more rapid and occurred earlier; at the end of the summer both plots had similar densities of born juveniles surviving.

Plot 3 in 1973 differed drastically from the 1973 control plot and from the decline seen on plot 3-1972. The number of juveniles born on plot 3-1972 declined in a similar way to what was observed on the control plot in 1972, although juvenile dispersal was proportionally reduced on plot 3 (Fig. 6). In 1973, only two juveniles were born and both remained on plot 3 until the end of the season (Fig. 5). These very small numbers precluded statistical comparison with other plots and years.

In 1973, 4 immigrant juveniles moved onto plot 1 which was the same number as observed in 1972 (Table 7); juvenile immigration in both years did not start until 8 weeks after mean juvenile emergence when only 18% of the born juvenile population were still present (Fig. 6). In plots 2 and 3, juvenile immigration started very much earlier in both years. The number of immigrants was not much different on plots 2 and 3-1973 from 1972, i.e. 4 on plots 2 and 3 in 1973, versus 4 and 6 in 1972 (Table 7). Immigrant juveniles on plot 2-1973 were 83% of the total juvenile population 12 weeks after mean juvenile emergence (Fig. 6). This was significantly greater (Chi-square, S.99.9) than in 1972 when after 11 weeks, they represented only 20%. In plot 3-1973, immigrant juveniles were 67% of the total juvenile population 6 weeks after mean juvenile emergence but this was not significantly greater than seen in 1972, when immigrant juveniles were 57% of the total juvenile population after 11 weeks.

Juvenile immigration occurred much earlier onto plots 2 and 3 in 1973 than onto the control plot. On the latter plot, immigrants never represented the large proportions of the total juvenile populations as seen on plots 2 and 3. The high numbers of juveniles born within the plot boundaries on plot 1 prevented immigration until quite late in the summer, when born juveniles were probably already going into hibernation.

5. Summary: adult and juvenile populations 1973

ADULT POPULATION

April 1973

1. The densities of squirrels on all plots in April 1973 were higher than in April 1972. The largest increase was seen on the plot having the lowest resident density in 1972 (plot 3), and the smallest on the plot having the highest 1972 resident density (plot 2).
2. The control plot (#1) had a significantly lower proportion of males than plots 2 and 3 which may have been related to the mestranol treatments given on plots 2 and 3 in 1972. Survival of juvenile males was better on a treated plot than on a non-treated plot.
3. Greater proportions of the April populations were composed of overwinter survivors on plots 1 and 2 than on plot 3. New squirrels were relatively more numerous on plot 3 than on plots 1 and 2.
4. Overall, survival of squirrels (adults and juvenile combined) was the same on all plots between April 1972 and 1973. Survival was the same for treated (0.35) and non-treated (0.32) squirrels when data from all plots was combined. However, within plot 2, treated squirrels had a higher survival rate (0.42) than non-treated squirrels (0.20). Overall, non-resident squirrels (0.27) survived as well as resident squirrels (0.37).
5. Overall, adults (0.33) survived better than juveniles (0.23) but adult (0.38) and yearling (0.39) females had the same survival rate. The adult-juvenile difference could possibly be attributed to a better survival of the adult males (0.17) over juvenile males (0.07). Females, both adult and yearling, survived better than males.

May 1973

6. Between April and May 1973, population numbers were reduced by a third in the two non-treated plots (#1,3) due to emigration and mortality, while remaining much the same on the treated plot (#2).
7. The population decrease seen between April and May on plots 1 and 3 in 1973 was significantly greater than noted in 1972 for the same period.
8. No change in numbers was seen between April and May on plot 2 in 1973, whereas numbers had increased on this plot in the same period of 1972. Immigration was reduced on plot 2-1973 by comparison to 1972. The

distribution of baits around the plot in 1973, as well as the general improvement of vegetation in the areas surrounding the plot, may both account for this decline of adult immigration. Immigration did not occur on plots 1 and 3, which did not differ significantly from what was observed on the plots in 1972.

9. Emigration/mortality over the period April to May was similar on all plots in 1973, despite their varied population densities and treatments.
10. The proportions of April-May populations establishing residency in May 1973 were the same on all plots despite differences in population densities and treatment given.
11. When success in establishing residency was compared between 1972 and 1973, no changes could be shown on plots 1 and 2 but were demonstrated on plot 3. Plot 2 was treated to a greater extent in 1973 but reduced immigration prevented the establishment of more squirrels. Plot 3 was treated in 1972 but not 1973; the proportion of squirrels which established residency was significantly reduced in 1973.
12. More squirrels became resident on the control plot in 1973 than in 1972, because more squirrels were present in the April populations. In plot 2, reduced immigration opportunities resulted in a smaller number of squirrels establishing residency in 1973. In plot 3, a greater mortality in April resulted in the plot having the same number of residents as in 1972, although initial population in April 1973 was much greater.
13. No difference was observed in the success of home burrow establishment between treated and non-treated squirrels on plot 2 in 1973.

June 1973

14. Return into hibernation occurred at similar times on all plots in 1973. Treated females still went into hibernation sooner than breeding females, and, as was the case in 1972, breeding status and body weight both contributed to the determination of average onset of hibernation.
15. Return into hibernation occurred earlier in 1973 than in 1972 for all groups of squirrels, i.e. breeding and non-breeding females and adult males.

JUVENILE POPULATION

16. Juveniles emerged earlier on the control plot than on plots 2 and 3 in 1973.
17. Juveniles were born in considerable numbers on the control plot in 1973, although the emergent litter size was slightly smaller (5.1) than in 1972 (6.9).
18. Natality was reduced on plot 2 in 1973, a result of extensive mestranol treatment and environmental factors. Emerging litter size was reduced both on plots 2 (2.0 versus 4.1 in 1972) and 3 (1.0 versus 2.0 in 1972), most likely as a result of bad weather and increased predation in 1973.
19. On the control plot, decline of born juvenile populations was the same in 1973 as in 1972, and immigrant juveniles were not able to move in until very late in the season; at that time, they only represented small proportions of the total juvenile population present on plot 1.
20. In plots 2 and 3, numbers of born juveniles were very low and immigrant juveniles moved in very early forming large proportions of the total juvenile populations. This situation was not different from what was seen in 1972. But the decline of born juveniles in these plots followed a pattern different from the one observed in the control plot, contrary to what was observed in 1972.
21. The proportion represented by immigrant juveniles was greater on plot 2 in 1973 than in 1972, while it did not differ on plots 1 and 3 between the two seasons.

D. Population 1974

1. Adult population: April 1974

Spring in 1974 was late; there was snow left on the ground as late as April 23, while all snow had gone by the end of March in 1972 and 1973. Squirrels were trapped between April 18 and 25. Although activity was reduced, all squirrels were trapped and marked after a few days and no new squirrels were observed. I believe that all squirrels had emerged and were present in the plots when trapping occurred since this was done a month after normal date of emergence (Section I.A).

a. Densities

In April 1974, 16, 9 and 3 squirrels were trapped on plots 1, 2 and 3 giving densities of 28, 13 and 4 squirrels per hectare (Table 5). These numbers represent decreases on all plots when compared to the numbers observed in April 1972 and 1973. Seventy-five percent, 45% and 30% of the adult densities observed in April 1972 were observed on plots 1, 2 and 3 in April 1974 (Fig. 4). The decline of density observed on plot 2 (Chi-square, S.99.5) and on plot 3 (Chi-square, S.99.5) was significantly greater than the decline seen on plot 1. The largest decrease in population density occurred on the plots that were previously treated. The effect was most dramatic in plot 3, where the concept of a 'colony' could not be applied to the three scattered squirrels left on this plot in 1974.

The extent of the decrease was related to the mestranol treatments given but also seems to be related to the previous year population densities. When compared to the 1973 April levels, 49%, 37% and 15% of the population numbers on plots 1, 2 and 3 were seen in April 1974 (from Fig. 4). The decreases observed in plots 1 and 2 were similar (Chi-square, N.S.); these plots had the same resident densities in 1973 (21.6 and 23.2 squirrels per hectare) (Table 5). Plot 3 had a resident density of only 12.3 squirrels per hectare in 1973, and the decrease in numbers on that plot was significantly greater than the decreases observed on plots 1 (Chi-square, S.99) and plot 2 (Chi-square, S.99). The lowest density plot from 1973 was thus characterized by the greatest decrease of the April 1974 population.

Two years after the first treatment was given to animals on plots 2 and 3, populations were reduced by half on plot 2 (approximately 50% treatment each year, initial high density), and by more than two thirds on plot 3 (treated only once at 80% in 1973, initial low density).

b. Sex ratio

In April 1974, the sex ratio did not differ significantly between plots as 3 males and 15 females were trapped on plot 1, 1 male and 8 females on plot 2, and the three squirrels caught in plot 3 were all females (Chi-square tests) (Table 5). The sex ratio observed on each plot did not differ significantly from that observed on these same plots in April 1972 and 1973.

c. Age distribution and population composition

In April 1974, the populations present on plots 1, 2 and 3 were composed of three groups: 1. adult survivors that were first trapped as adults in 1972 or 1973 (age classes 1 and 3), or first trapped as juveniles in 1972 (age class 2), 2. juveniles born in 1973 (age class 4), and 3. new squirrels never trapped previously, also considered as adults but of unknown age (age class 5) (Table 8). The proportions of adult survivors were not significantly different between plots (Chi-square tests) (Table 9). Neither the proportions of juveniles born in 1973 and surviving to April 1974 nor the proportions of newcomers were significantly different between plots (Chi-square tests, N.S.). It is interesting to note that no new squirrels were found on plot 3 which is astonishing as only 3 adult squirrels were resident there in April 1974.

The proportions of the different classes of squirrels found on each plot in April 1974 did not differ significantly from those observed in April 1973 (Chi-square test, N.S.), with the exception of plot 3. In plot 3-1974, the proportion of new adults, i.e. immigrants, was reduced to zero, being significantly smaller than in 1972 (60%) (Table 9; Chi-square, S.99.9). This seems to indicate that the squirrel population surrounding this plot was no longer able to replenish the depleted population found on plot 3.

i. Survival 1972 to 1974

None of the squirrels trapped as adults in 1972 (age class 1) were left on plot 3 by April 1974, although two and five females were left on plot 1 and plot 2 respectively (Fig. 4). Interestingly, all 5 females on plot 2 had previously been treated with mestranol, but their survival rate was not significantly different from that of non-treated females on plot 1. A few of the juveniles born in 1972 were left on plots 1 and 3 in April 1974, while none survived on plot 2 (Fig. 4). Their survival was better on plot 1 than on plot 2 (Chi-square, S.95). It is not known if this fact is related to the mestranol treatment given on plot 2.

ii. Annual survival 1972-1973, compared to 1973-1974

As was the case in April 1973, annual survival rates in April 1974 were the same on all plots, both for the groups of adult and juvenile squirrels (from Table 11; Chi-square tests, N.S.). The survival rate on the 1973 treated plot (#2) was not any different from those on the non-treated plots (#1,3). However, overall, the 1973-1974 annual survival was lower than it was in 1972-1973, and this both for adults (0.22 versus 0.33; Chi-square, S.95) and juvenile (0.08 versus 0.23; Chi-square, S.99.9) groups of squirrels (Tables 10, 11). This could be related to the harsher climatic conditions observed during the 1973-1974 winter and spring.

It was shown that on plot 2 in April 1973, treated squirrels survived better than non-treated squirrels (Section III.B.2.c). However, so few ground squirrels were left unaffected by the drug on plot 2-1973, that it was impossible to check this relationship between April 1973 and 1974.

Residents (0.35) survived better than non-residents (0.11) over the 1973-1974 winter (Table 11; Chi-square, S.99.5). This relationship could not be shown in April 1973 (Section III.C.1.d). Interestingly, it was the squirrels the most familiar with the plot, i.e. the residents, that survived best in the harsher climatic conditions of 1973-1974.

As was the case in April 1973, adults (0.22) survived better than juveniles (0.08) (Table 11; Chi-square, S.99.5) and females (0.21) survived better than males (0.01)(Table 11; Chi-square, S.99.9). However the harsher 1973-1974 survival conditions may have brought a difference. While adult and juvenile females had the same survival in 1972-1973 (Section III.C.1.d), in April 1974, it was shown that adult females survived better (0.28) than juvenile females (0.12) (Table 11; Chi-square, S.97.5). This difference was observed only on the control plot (#1) and not in the two previously treated plots (#2,3). In the two latter plots, densities were reduced by the

Table 11. Annual survival of adult and juvenile ground squirrels initially trapped in 1972 and 1973 on plots 1, 2 and 3, and still present on these plots in April 1974.

SURVIVAL

number of squirrels belonging to a given 1972 or 1973 cohort and surviving to April 1973, divided by the total number of squirrels belonging to the same cohort in 1972 or 1973

COHORTS OF SQUIRRELS AND 1973 STATUS	PLOT 1			PLOT 2			PLOT 3			ALL PLOTS		
	Female	Male	total	Female	Male	total	Female	Male	total	Female	Male	total
ADULTS, first trapped in 1972 and 1973	0.31 (35)	0 (3)	0.30 (38)	0.32 (19)	0 (10)	0.21 (29)	0.14 (14)	0 (6)	0.10 (20)	0.28 (68)	0 (19)	0.22 (87)
a.1. age class 1 (3 years+)	0.29 (7)	0 (2)	0.22 (9)	0.56 (9)	-	0.56 (9)	0 (4)	0 (1)	0 (5)	0.35 (20)	0 (3)	0.30 (23)
a.2. age class 2 (2 years)	0.43 (14)	-	0.43 (14)	0 (6)	0 (4)	0 (10)	0.33 (3)	- -	0.33 (3)	0.30 (23)	0 (4)	0.26 (27)
a.3. age class 3 (2 years+)	0.21 (14)	0 (1)	0.20 (15)	0.25 (4)	0 (6)	0.10 (10)	0.14 (7)	0 (5)	0.08 (12)	0.20 (25)	0 (12)	0.14 (37)
b.1. residents in 1973*	0.50 (14)	-	0.50 (14)	0.46 (13)	- (3)	0.37 (16)	0.12 (8)	0 (2)	0.10 (10)	0.40 (35)	0 (5)	0.35 (40)
b.2. non-residents in 1973 *	0.19 (21)	0 (3)	0.17 (24)	0 (6)	0 (7)	0 (13)	0.17 (6)	0 (4)	0.10 (10)	0.15 (33)	0 (14)	0.11 (47)
c.1. treated in 1973 *	-	-	-	0.33 (9)	0 (4)	0.23 (13)	-	-	-	0.33 (9)	0 (4)	0.23 (13)
c.2. non-treated in 1973*	0.31 (35)	0 (3)	0.29 (38)	0.30 (10)	0 (6)	0.19 (16)	0.14 (14)	0 (6)	0.10 (20)	0.27 (59)	0 (15)	0.22 (74)
JUVENILES born in 1973 age class 4	0.07 (40)	0.03 (35)	0.05 (75)	0.33 (6)	0 (4)	0.20 (10)	0.33 (3)	0 (3)	0.17 (6)	0.12 (49)	0.02 (42)	0.08 (91)

1, 2, 3, 4: age classes, ( ) : total number of squirrels belonging to a given age class in 1973,
*: from Table 6

previous treatment and either, juvenile females had as many chances of survival as adult females, or else numbers were too low to show such a difference.

Survival of adults was the same on plots 1 and 2 during the 1972-1973 and 1973-1974 winters (Tables 10, 11; Chi-square tests, N.S.). These two plots basically received the same treatment or non-treatment in 1972 and 1973 (Table 1). However, plot 3 that was treated in 1972 but was not in 1973, saw a significant reduction in the survival rates of its adult population - 0.45 from April 1972 to April 1973, versus 0.10 between April 1973 and April 1974 (Tables 10, 11; Chi-square, S.99.5). This seems to support the 1972-1973 evidence that overall, treated squirrels may have better survival rates than non-treated squirrels. This could be related to the fact that treated squirrels accumulate fat faster than non-treated squirrels. Squirrels that are heavier in June survive better than lighter squirrels (D.R. Michener, 1972).

Juvenile survival dropped drastically in 1974 on the control plot when compared to the previous year's survival (Chi-square, S.99.9). This was not observed on plots 2 and 3 (Chi-square tests, N.S.). As a result of the low densities on plots 2 and 3 in 1973 (Table 7), juveniles were possibly better prepared to face the harsh conditions of the winter and spring of 1974 than juveniles from the high density population on the control plot .

2. Summary: Adult population 1974

ADULT POPULATION

April 1974

1. In April 1974, adult populations were reduced on all plots compared to the populations observed on these same plots in April 1972. However, the decrease was significantly greater on the two plots that were previously treated with mestranol. The largest decrease was also characteristic of the least dense plot (#3). Sex ratio was the same on all plots.
2. The same proportions of adult and juvenile survivors, and of new squirrels were found on all plots.
3. On plot 3-1974, there was a significant decrease in the proportion of new adults when compared to what was observed in April 1973. This tends to indicate that the surrounding squirrel population could no longer compensate for the losses experienced by plot 3.
4. Five (from 25) of the 1972 adult females survived to April 1974 on plot 2; all of them were previously treated. Only 2 (from 18) of the 1972 non-treated adult females from plot 1 survived to 1974. No difference in survival could be shown.
5. Annual survival for adult and juvenile squirrels was the same on the treated and non-treated plots between April 1973 and April 1974.
6. On the control plot, survival in 1973-1974 was significantly lower than in 1972-1973. Resident (0.35) and adult (0.22) squirrels seemed to survive better the harsher conditions encountered during the 1974 winter than did the non-resident (0.11) and juvenile (0.08) squirrels.
7. On plot 3, adult survival was lower during 1973-1974 than during 1972-1973, whereas it was similar on plots 1 and 2 in both years. No treatment was given in plot 3 in 1973 as opposed to a 78% treatment in 1972. This could indicate that treated squirrels survived better than non-treated squirrels on this plot.
8. On low density plots, such as plots modified by mestranol treatment, juveniles did not suffer as much from the harsher conditions as juveniles from the high density control plot; their survival remained the same in 1974 as in 1973, while it dropped on the control plot.

E. Overview: adult and juvenile populations 1972-1974

1. Populations 1972

The mestranol treatment of 1972 prevented the successful breeding of 96% of all treated females (Section I.A). The number of juveniles per resident female was lower on the control plot (6.9) than on plots 2 (2.4) and 3 (0.7) respectively (Table 7). However, this reduction in natality was compensated for in many ways both in the adult and juvenile populations.

Between April and May, the adult population present on the control plot decreased, while those from the treated plots either increased (plot 2) or remained stable (plot 3). Not only were more adult squirrels left in May on the treated plots, but proportionally more established territories within the plots. Moreover, more immigration occurred onto the treated plots and immigrants, most of them females, further increased the reproductive potential of the plots receiving them (plot 2 only). However, non-breeding squirrels, i.e. those sterilized with mestranol, were more successful than non-treated squirrels in maintaining themselves as resident on a plot (#2), thus occupying burrows that presumably could have been used by more breeding squirrels. Treated females returned into hibernation earlier than non-treated females of similar body weight. Therefore, adult populations on the treated plots were reduced when juveniles were attempting to establish a home burrow, which may contribute to the higher ingress of juveniles on the treated plots.

In effect, immigration of juveniles occurred much earlier onto the treated plots and immigrants represented larger portions of the juvenile populations in these plots for most of the summer when compared with the control plot. On the control, immigration occurred only when resident juveniles were already going into hibernation. Thus the reduced natality produced by the mestranol treatment was compensated for within the juvenile populations themselves. However, the questions remains as to whether or not the compensation was adequate to fully replenish what would have been the normal populations of juveniles in the treated plots.

It was shown that the mestranol treatment affected the number of squirrels establishing territories in treated plots and that it limited the number of females breeding, and possibly affected the litter size.

Consequently, it is impossible to estimate the number of juveniles that would have been born on plots 2 and 3 if no treatment had been given. It is not known how many females would have been present to breed or how many juveniles would have been born to them. Moreover, it is not possible to determine how many of these juveniles would have been left at the end of the summer.

Two numbers can be used to estimate a possible compensation for the mestranol treatment. The first was the number of adult squirrels present in the plots in early April; these numbers were not affected by the mestranol treatment and should give a measure of the carrying capacity of each plot. The second number was the population of juveniles left in the plots 8 weeks after mean juvenile emergence. This number of juveniles was a result of all compensation factors that could act up to that point in either the adult or juvenile populations. In addition, at that time most of the adults had gone into hibernation (Table 2) so that any difference in adult behavior or numbers had no further effect; juvenile populations were then a function of the juveniles' behavior and numbers. Also no juvenile had gone into hibernation at this time (Table 2); the numbers of juveniles observed should be a function of their ability to compensate for treatment and be limited only by the carrying capacity of the plots.

Numbers of adults present in early April and numbers of juveniles present 8 weeks after mean juvenile emergence are given in Table 12; a ratio calculated between these counts and the densities can be compared. The ratio (B/A) was 1/1 in all plots indicating that there were as many juveniles in July as there were adults in April. This would tend to indicate that at both times, the number of squirrels present was a function of the carrying capacity of each plot, or at least of the surrounding area, and that possibly at both times, an equilibrium was reached between the space available and the number of squirrels. This ratio was the same for all plots notwithstanding the mestranol treatment given in early April; it thus seems that the populations on the treated plots, through the means mentioned above, had compensated for the reduction of the juvenile populations brought about by the treatment. Furthermore, densities were quite similar at both these times (Table 12).

Table 12. Estimate of compensation for the mestranol treatment as seen in the juvenile populations present on plots 2 and 3 in 1972.

	Plot 1	Plot 2	Plot 3
A. Number of adult squirrels present in April	24	20	10
Density (x/hectare)	37	29	12
B. Number of juvenile squirrels left 8 weeks after mean juvenile emergence	26	23	10
Density (x/hectare)	40	33	12
C. Ratio (B/A)	1.1	1.1	1.0

Compensation for the reduced natality resulting after mestranol treatment was thus achieved on plots 2 and 3 themselves. However it should be remembered that by choice each plot was a more desirable spot than the area surrounding it; thus squirrels are naturally drawn towards them and any dead or emigrating squirrel should be readily replaced from neighbouring populations. However, the numbers of juveniles born in the whole area was reduced when treatment was given and over a period of time these areas would have a much lower number of potential immigrants compared to the area surrounding the control plot. In effect, the juvenile population is the pool from which populations are replenished as mortality takes its share; if this pool is reduced, the abiltiy of a given population to cope with mortality would ultimately be lessened. The treatments given in the populations surrounding plot 3 in 1972 and plot 2 in 1973 no doubt also had the effect of further reducing the total number of potential immigrants for these plots.

2. Populations 1973

In the 1973 treated plot, i.e. plot 2, residency success was still higher for treated squirrels, but adult immigration was much reduced and as a result, the number of non-treated squirrels resident that year was much reduced as compared to 1972. These few non-treated squirrels all bred, but the emerging litter size was reduced by predation and bad weather. Thus very few young emerged on plot 2 in 1973. Immigrant juveniles were few although they represented large proportions of the total juvenile population. Adult and juvenile immigration may have been limited in 1973 due to the mestranol treatment given around plot 2 and also as a result of the improved vegetation conditions characterizing the whole study area. Thus less squirrels were available to move in in comparison to 1972. In August 1973, 8 weeks after mean juvenile emergence, only 5 juveniles were left on plot 2.

In plot 3-1973, residency success and adult immigration were the same as on the control plot and the same number of juveniles immigrated as in 1972 . However, the population of juveniles emerging on plot 3 was reduced drastically , a result it was thought of predation and poor weather. Only 5 juveniles were left 8 weeks after mean juvenile emergence in this plot. In contrast, 27 juveniles were left on the control plot (#1) at the same time (Table 13).

The number of juveniles left in August 1973 cannot be compared to the April 1973 adult populations as I have shown that on plots 2 and 3, such adults had been affected by the previous year mestranol treatment. Thus overall, the April 1972 adult populations still provide the only guideline for comparison, since they were unaffected by any treatment. Ratios were established between the number of adults present in the April 1972 and 1973 populations and the number of juveniles left 8 weeks after mean juvenile emergence in 1973. These are shown in Table 13.

When using the April 1972 adult numbers (A) and comparing the resulting juvenile-adult ratio (D) to that observed in 1972 (Table 12), it can be seen that on the control plot, the same ratio was observed each year, i.e. 1.1 (Tables 12 and 13). By contrast on plot 2, a plot twice treated (Table 1), the ratio was only 0.25 in 1973 while it was the same as in the control plot in 1972 , i.e. 1.1 (Table 12). In plot 3, a plot treated only

Table 13. Estimate of compensation for the mestranol treatment as seen in the juvenile populations present on plots 2 and 3 in 1973.

	Plot 1	Plot 2	Plot 3
A. Number of adults present in April 1972	24	20	10
B. Number of adults present in April 1973	37	24	20
C. Number of juveniles left 8 weeks after mean date of juvenile emergence	27	5	5
D. Ratio (C/A)	1.1	0.25	0.50
E. Ratio (C/B)	0.73	0.20	0.25

once, juvenile- adult ratio was 0.50 in 1973 as compared to a value of 1.0 in 1972 (Tables 12 and 13). The ratio (E) comparing the 1973 adult to juvenile populations also shows the lack of breeding success characterizing the non-treated populations. While both plots 2 and 3 had compensated for their losses in 1972, such was not the case in 1973. The greatest loss occurred in plot 2, where the juvenile population in 1973 was only a fifth of that observed in 1972; on plot 3, the juvenile population had been reduced to half the numbers observed at the same time in 1972 (Tables 12 and 13).

When the proportions of adults (April) and juveniles (8 weeks after mean emergence) present in 1973 are compared to what they were in 1972 (Tables 12 and 13), it is seen that the juveniles proportions observed in 1973 were significantly reduced in plot 2 (Chi-square, S.99.9), while they were the same in plots 1 and 3 each year (Chi-square tests, N.S.). It can thus be concluded that plot 2 was not compensating anymore for the losses incurred in 1972 and 1973 as a result of the natural mortality causes, but especiallly as a result of the mestranol treatments given. The treatments had most likely destroyed the surplus that normally allows a population to recover from natural losses. This is also probably the case in plot 3, although the losses were not as drastic. It is likely that the small numbers of squirrels involved in that plot precluded the demonstration of any statistical differences.

3. Populations 1972-1974

Within each year, compensatory mechanisms were at work to alleviate the reductions produced in the plots by natural mortality factors, as well as by the mestranol treatments given. The control population seemed to fluctuate as a function of the food supply available as determined by weather, and other mortality factors such as predation. Plots 2 and 3, which were treated once or twice, were also submitted to these natural losses but also had a reduction of their populations as a result of the mestranol treatments given. It is postulated that the fluctuations observed on the control plot are within the bounds imposed by the natural environment and that surplus squirrels were always available to allow a maximal utilization of the habitat. As a result, more adults than needed were present every spring so that all home areas allowed by the current food supply could be filled. Many more juveniles than needed to use the available space or food were born each year to compensate for normal and possibly greater than normal mortality during the summer (predation, rain) or winter (harsh winter). In plots 2 and 3, losses resulting from the mestranol treatments were compensated for 1. by greater adult and juvenile immigration, 2. by lowered adult and juvenile dispersal and 3. by improved adult and juvenile survival. I feel however that the ability of these plots to compensate for natural and imposed losses was effectively destroyed. As a result, plots 2 and 3 were no longer able to sustain the losses incurred through predation, overwinter mortality, dispersal, etc. and their numbers consequently declined. It is proposed to summarize here the population fluctuations experienced by the three plots between April 1972 and 1974, using the April 1972 adult populations as a baseline. Only at that time were all populations unaffected by mestranol treatment. These fluctuations are summarized in Table 14.

Table 14. Fluctuations of the adult and juvenile populations found on plots 1, 2 and 3 during 1972, 1973 and 1974. The adult populations of April 1972 are used as a baseline (100%) for comparisons.

	Plot 1	Plot 2	Plot 3
<u>April 1972</u>			
1. adult cohort	100 (24)	100 (20)	100 (10)
<u>May 1972</u>			
2. adult residents	46 (10)	105 (21)	100 (10)
3. juvenile cohort	245 (59)	225 (45)	120 (12)
<u>July 1972</u>			
4. juvenile cohort	108 (26)	115 (23)	100 (10)
<u>April 1973</u>			
5. adult cohort	154 (37)	120 (24)	200 (20)
<u>May 1973</u>			
6. adult residents	58 (14)	80 (16)	100 (10)
7. juvenile cohort	312 (75)	50 (10)	60 (6)
<u>July 1973</u>			
8. juvenile cohort	112 (27)	25 (5)	50 (5)
<u>April 1974</u>			
9. adult cohort	75 (18)	45 (9)	30 (3)

* : number of juveniles left in each plot 8 weeks after mean date of juvenile emergence , ( ) : number of squirrels involved.

It is assumed that a basic number of 100 squirrels were present in each plot in April 1972 (1). In May 1972, surpluses were reduced sharply on the control plot as home areas were established in response to the habitat conditions prevailing then (2). In the treated plots, the numbers of squirrels were not reduced in such a manner; all the squirrels present in April and still alive in May, established home areas as did large numbers of immigrant adults (2). This was seen as the first compensation offered by these populations to the treatments given. In May, the control plot produced a large juvenile cohort. Plot 2, treated at 50% but having already compensated somewhat by having a greater than expected adult resident population, succeeded in producing a juvenile cohort equivalent to the one seen on the control plot (3). Plot 3, having received a more intensive treatment, was not so successful and its juvenile cohort was only half of that observed on the two other plots (3). However, compensation occurred in the juvenile populations themselves, so that at the end of the summer, juvenile populations were equivalent on all plots (4). Winter was relatively mild in 1972-1973, and all April 1973 populations had increased when compared to the April 1972 levels, especially on plot 3 (5). More residents established home areas on the control plot, while reduced immigration on plot 2 and increased mortality on plot 3 either maintained or slightly reduced their resident populations when compared to the May 1972 levels (6). Already, the treated plots were seemingly losing their ability to compensate for incurred losses. Again the control plot produced a large juvenile cohort in May 1973. Plots 2 and 3 failed to do so however, and their juvenile cohorts were only fractions of their baseline populations (7). Again, plots 2 and 3 were failing to compensate for the losses incurred through natural reduction factors or resulting from the treatment. By July 1973, the juvenile cohort on the control plot was comparable to the one observed in July 1972, while in plots 2 and 3, juvenile populations were only fractions of their 1972 levels (8). In April 1974, all populations were reduced, probably as a result of the harsh 1973-1974 winter conditions (9). However, the control plot still had enough squirrels to fill the home areas available, while both plots 2 and 3 were left with much reduced numbers of squirrels. Surrounding populations had also been depleted by the mestranol treatments given the previous years, and by the harsh 1973-1974 winter conditions. The surrounding area populations were no longer able to compensate for the losses incurred by plots 2 and 3, nor were the populations on these plots able to make maximal use of their habitat.

RESULTS PART IV. SOCIAL BEHAVIOR

A. Introduction

Social organization may be analyzed in terms of social relationships between individuals. Such relationships follow a predictable pattern within a given population and are established through regular behavioral contacts between two or more individuals. Some contacts increase the tendency of the social members to remain together, and thus are described as cohesive (King, 1955). Other types of interactions tend to spread the individuals throughout their habitat as is the case for territorial types of behavior; such interactions are described as agonistic (Scott, 1956 and 1958).

Many cohesive and agonistic types of interactions were observed in populations of Richardson's ground squirrels and have been described in detail by Quanstrom (1968 and 1971), Yeaton (1969 and 1972), Clark (1969), Clark and Denniston (1971), Sheppard and Yoshida (1971), Whyte (1971) and Michener (1971). All the types of interactions described in these previous studies were not recorded in my investigation as the purpose of this work was to quantify certain types of behavior and not to give a detailed description of them. The types of interactions used to quantify social behavior in the present study were described in the Material and Methods section. Social relationships in populations of Richardson's ground squirrels were investigated by G.R. Michener (1972), and Michener and Sheppard (1972). Social structure was described by some of the same authors (Yeaton, 1972; Wehrell, 1973; Michener, 1973b and 1973c).

The cohesive and agonistic relationships observed between different groups of ground squirrels will be described here, and their intensities compared. Comparisons will be made between treated and non-treated plots or squirrels, and for adult to adult, adult to young, and young to young interactions. Comparisons will also be made between seasons.

The numbers of juveniles present on plots 2 and 3 in 1973 were so reduced in May 1973 (Fig. 5) that it was judged necessary to establish three more plots to obtain additional data on juvenile behavior; in effect, no more interactions were observed then among juveniles on plots 2 and 3 (Fig. 7). Subsequently, 64 45-minute observation periods were made on plots 4, 5 and 6 between June 2 and August 28, 1973 (App. 2). While data on social behavior among juveniles, and between juveniles and adults will be discussed from all six plots, interactions among adults will be described mostly for adults from plots 1, 2 and 3. By the time that behavioral observations started on plots 4, 5 and 6, most adult-adult interactions had already taken place, juveniles had already emerged and juvenile parentage was unknown. Data on adults and juveniles on these plots did not match data from plots 1, 2 and 3 in precision. This is why sometimes, data from plots 4, 5 and 6 will be discussed separately, but will be compared to plot 1 for reference.

B. Cohesive behavior

A total of 354 cohesive interactions were recorded on plots 1, 2 and 3 during the field seasons 1972 and 1973 (App. 3) in a total of 234 45-minute observation periods (App. 2). Similarly, 185 cohesive acts were counted on plots 4, 5 and 6 (App. 3) after 64 observation periods (App. 2). These interactions will be analyzed here in relation to their frequency between different age and sex classes of squirrels and in relation to their timing in the annual cycle. The nature of these interactions will be briefly given.

1. Adult-adult interactions

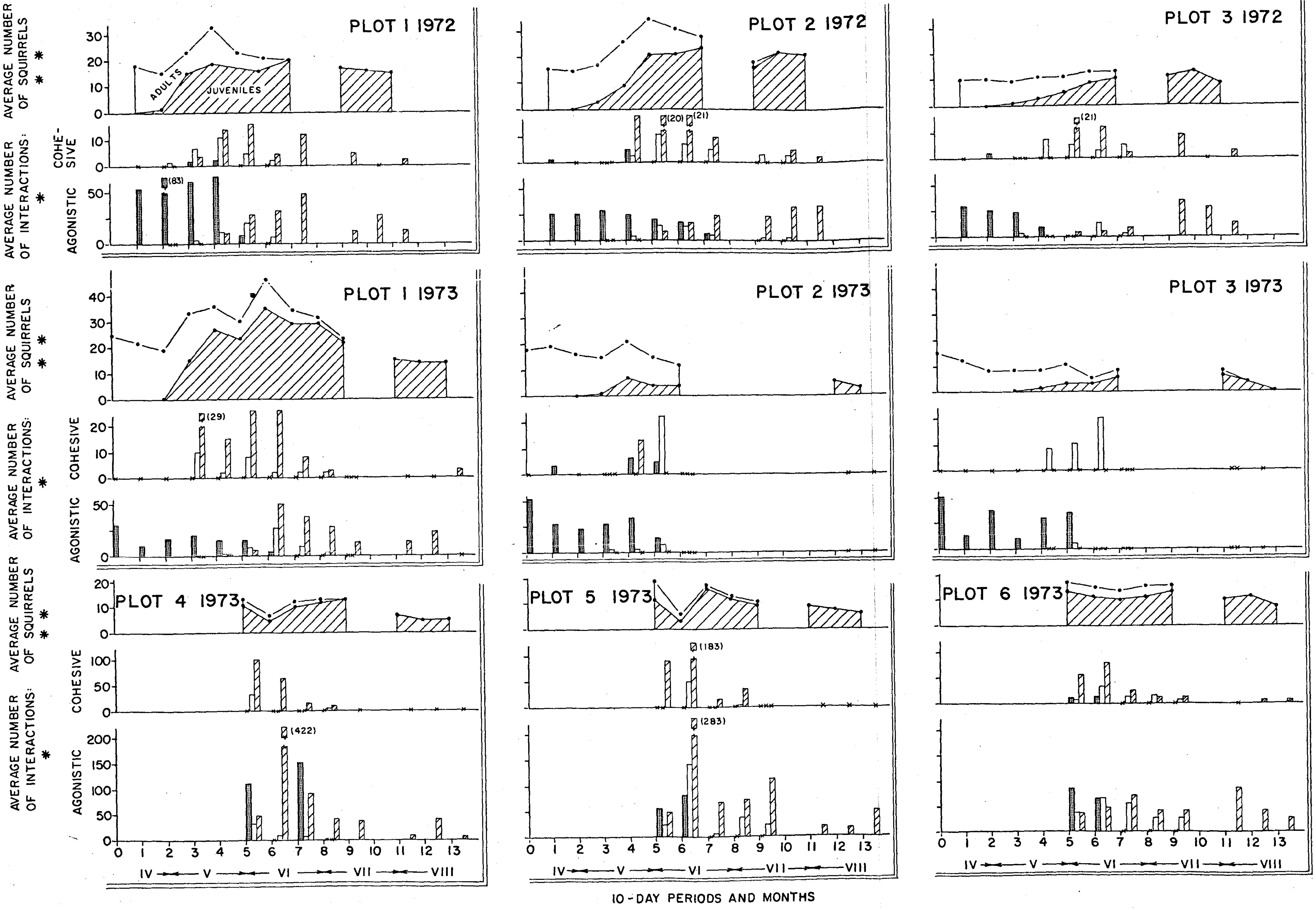
Only thirteen cohesive interactions were observed between adults on plots 1, 2 and 3 during the 1972 and 1973 seasons, representing less than 4% of the cohesive acts recorded (App. 3). Adult cohesive behavior consisted of social grooming (38%), nose contacts (31%), kisses (15%) and positive association (15%) (from App. 9A).

Cohesive behavior was rare and sporadic among adult squirrels and occurred only between mid-April and the beginning of June each year (Fig. 7). During that period, home areas were well established, young were born and females were busy feeding them. By the middle of May, juveniles had begun to emerge from the maternal burrow but were still confined to their mother's home area.

No differences in cohesive behavior could be shown between plots in 1972 and 1973 (Mann-Whitney tests). Similarly, there was no difference within any plot between the 1972 and 1973 seasons. The maximum levels of

Figure 7. Average numbers of Richardson's ground squirrels, and of cohesive and agonistic interactions observed on plots 1, 2, 3, 4, 5 and 6 during 1972 and 1973

—●—	average number of active adult and juvenile squirrels observed during a 45-minute observation period
▧●▧	average number of active juvenile squirrels observed during a 45-minute observation period
▒	average number of adult-adult interactions observed per 100 squirrels during a 45 minute observation period
▯	average number of adult-young interactions observed per 100 squirrels during a 45-minute observation period
▨	average number of young-young interactions observed per 100 squirrels during a 45-minute observation period
—x—	an 'x' on the horizontal axis indicates that squirrels belonging to a given group were present, but did not interact
*	number of interactions per 100 squirrels per 45-minute observation period
* *	number of squirrels per 45-minute observation period


PLOT 1 1972
PLOT 2 1972
PLOT 3 1972
PLOT 1 1973
PLOT 2 1973
PLOT 3 1973
PLOT 4 1973
PLOT 5 1973
PLOT 6 1973
AVERAGE NUMBER OF SQUIRRELS *
*
AVERAGE NUMBER OF INTERACTIONS: *
COHESIVE
AGONISTIC
ADULTS
JUVENILES
(83)
(20)
(21)
(21)
(29)
(183)
(422)
(283)
0 10 20 30 40
0 10 20 50 100 150 200
0 1 2 3 4 5 6 7 8 9 10 11 12 13
IV V VI VII VIII
10-DAY PERIODS AND MONTHS

cohesive interactions among adults were observed on plot 2 in both years (Fig. 7; Table 15). Seven of 9 cohesive acts observed on this plot involved mestranol treated squirrels (App. 3). However, as a result of the low number involved, a Mann-Whitney ranking test failed to show any significant difference between treated and non-treated squirrels (Table 15). The maximum level of cohesive interactions among adult squirrels occurred on plot 2, where adult density was highest (Table 5) but where at least 50% of the squirrels were sterilized (Table 1). However, though treatments and densities changed between plots and years, no differences could be demonstrated between intensities of adult cohesive behavior (Fig. 7).

The identity of many squirrels which had been trapped and marked the previous year was known in 1973. As a result, it was possible to establish that cohesive interactions among adults occurred mainly between related squirrels or between neighbours. Two yearling females, born from the same litter in 1972 and occupying adjacent territories in 1973, were seen to groom each other. An adult female was seen relating cohesively towards two yearling squirrels that were born in a territory adjacent to her own in 1972, and were still her neighbours in 1973. In every case of cohesive behavior among adults, the squirrels were occupying adjacent territories. Adult females, treated or not, related cohesively to each other and to adult males; the latter were not seen behaving cohesively among themselves.

2. Adult-young interactions

a. Plots 1, 2 and 3

Adults and juveniles were observed to behave cohesively towards each other on 139 occasions on plots 1, 2 and 3. This represents 39% of all cohesive acts observed on these plots during 1972 and 1973 (App. 3). Mothers were seen in a positive association with their own young, accounting for 40% of all adult-young cohesive interactions observed, and these females were either grooming (14%), kissing (10%), nosing (8%), or playing (4%) with their offspring (from App. 9A). Juveniles also associated with neighbouring adults (11%), although to a lesser extent, establishing nose contacts (8%), kissing (1%) and being groomed (3%) or occasionally playing (1%) with them (from App. 9A).

Table 15. Average number of cohesive interactions involving adults observed for different groups of ground squirrels (per 45-minute observation period, per 100 squirrels).

	PLOT 1		PLOT 2							PLOT 3						
10-day period	AA	AY AownY	AA	AM MA	MM	AA,AM MA,MM	AY AownY	MY	AY AownY MY	AA	AM MA	MM	AA,AM MA,MM MA	AY AownY	MY	AY AownY MY
1972																
1	0	-	0	0	3	1	-	-	-	0	0	0	0	-	-	-
2	0	1	0	0	0	0	-	-	-	0	2	0	2	-	-	-
3	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	3	11	2	3	0	5	2	1	2	0	0	0	0	8	5	7
5	0	4	0	0	0	0	10	2	10	0	0	0	0	3	5	6
6	0	2	0	0	0	0	7	0	7	0	0	0	0	3	0	3
7	-	-	0	-	-	0	5	-	5	0	-	-	0	5	-	5
9	-	-	0	-	-	0	2	-	2	-	-	-	-	-	-	-
10	-	-	0	-	-	0	1	-	1	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10-day average	0.8	5.0	0.2	0.5	0.5	0.7	3.9	0.7	3.9	0	0.3	0	0.3	3.8	2.5	4.2
1973																
0	0	-	0	0	0	0	-	-	-	0				-		
1	0	-	0	2	5	3	-	-	-	0				-		
2	0	-	0	0	0	0	-	-	-	0				-		
3	0	10	0	0	0	0	0	0	0	0				-		
4	0	2	0	0	6	6	0	0	0	0				8		
5	0	8	6	0	0	4	24	8	23	0				10		
6	0	1	0	-	-	0	0	-	0	0				20		
7	0	1				NO				0				0		
8	0	1				NO								NO		
9	0	0				NO								NO		
11	-	-				NO				-				-		
12	-	-	-	-	-	-	-	-	-	-				-		
13	-	-	-	-	-	-	-	-	-	-				-		
10-day average	0	3.3	0.9	0.3	1.8	1.9	3.4	2.7	5.7	0				9.5		

NO : no observations made; - : this group of squirrels was not present then
0 : the squirrels concerned were present but did not interact

Of all the interactions observed on the non-treated plots, 85% of all adult-young interactions occurred between mother and offspring, and only 15% were between juveniles and non-related adult squirrels (from App. 3). The fact that juveniles relate more often to their mother than to strange adults was also observed by Michener and Sheppard (1972) in field and laboratory situations. By contrast on the treated plots, 43% of the adult-young cohesive interactions occurred between juveniles and their adult male or female neighbours, while only 57% were observed between mother and offspring (App. 3). These ratios differ significantly from the control (Chi-square, S.99.9).

Juveniles in the treated plots received as much attention from the adults as juveniles from the non-treated plots. When the average numbers of adult-young cohesive acts per adult and juvenile (Table 15) or per juvenile only, were compared with Mann-Whitney tests, no significant difference was determined between treated and non-treated plots. On average, each juvenile and adult squirrel interacted cohesively towards each other on 5.0, 3.9 and 4.2 occasions on plots 1, 2 and 3 during the 1972 season, while they did so 3.3, 5.8 and 9.5 times in 1973 (Table 15); no significant difference exists between any of these numbers (Mann-Whitney tests). Mestranol-treated squirrels did not behave more cohesively towards juveniles than non-treated adult squirrels that were not related to the juveniles (Mann-Whitney tests, calculated from App. 3 and 5).

In 1972, the maximum of total cohesive interactions occurred 20 days after the first emergence of juveniles on all plots, which corresponded with the greatest combined number of active adult and juvenile squirrels observed on each plot (Fig. 7). Adult-young interactions on all plots started 10 days after first emergence of the juveniles, soon reached a maximum and then declined to zero after 40 days on plots 1 and 3 (Fig. 7). During this time, i.e. from mid-May until the third week of June, juveniles had emerged and become more independent of their mothers. Adult females spent more time feeding and responded less to their offspring. Additionally, juvenile ground squirrels were increasing their area of activity further from the maternal burrows. By the end of June, the vast majority of adult squirrels had gone into hibernation (Table 2) so that no more adult-young interactions were observed above ground (Fig. 7). While no adults were left on plots 1 and 3 after the end of June, in July one or two late breeding females were still active on plot 2. These females still behaved cohesively to their offspring (Fig. 7).

In 1973, adult-young cohesive interactions occurred between mid-May and the first 10 days of July and, as occurred in 1972, peaked during the first 20 days of June (Fig. 7). The peak of cohesive behavior coincided with the presence of the largest numbers of adult and juvenile squirrels being active on the control plot (#1), while it lagged by 10 days on plot 2, and actually corresponded to a low in squirrel numbers on plot 3 (Fig. 7). The low numbers of juveniles which were present on the latter two plots tended to over-emphasize the few interactions which actually occurred on these plots (see App. 3). As in 1972, no significant difference of adult-young cohesive behavior was observed between plots during the 1973 season and no difference was seen within any plot between 1972 and 1973 (Mann-Whitney tests).

b. Plots 4, 5 and 6

Behavioral observations started in early June on plots 4, 5 and 6 (Fig. 7). The full pattern of adult-young interactions was not seen on these three plots. Plot 6 did show a similar pattern which lagged some 10 days behind that observed on plot 1 (Fig. 7). In effect, the intensity of adult-young cohesive interactions increased, peaked and declined as the number of adult squirrels active above ground changed (Fig. 7). Only on plot 4 did the peak of cohesive behavior coincide with the maximum combined numbers of squirrels active on the plots (Fig. 7).

Plots 4, 5 and 6 respectively averaged 9.2, 10.4 and 15.2 adult-young cohesive interactions per 100 squirrels between June 1 and July 20 while the control plot (#1) averaged only 2.2 acts during the same time period (from Table 15). However, neither plots 4, 5 or 6 differed significantly from the control plot, and neither did they differ from each other. Thus, cohesive behavior on these plots did not differ in timing or intensity from plot 1.

3. Young-young interactions

a. Plots 1, 2 and 3

On plots 1, 2 and 3 during 1972 and 1973, a total of 202 cohesive interactions were observed between juveniles, i.e. 57% of all cohesive acts observed (App. 3). The most prevalent type of cohesive interaction among young was playing (52%). Juveniles were seeking each others company (22%), kissing (9%), grooming each other (4%) or establishing nose contact (13%) (from App. 9A).

Since juveniles were also involved in 139 cohesive interactions with the adults present, they participated in a total of 96% of all cohesive interactions observed on plots 1, 2 and 3 in 1972 and 1973 (App. 3). But the intensity of cohesive behavior between adults and young, and between young only was not significantly different. Adult-young cohesive interactions averaged 5.3 acts (per 100 squirrels per 45-minute period) on plots 1, 2 and 3 during 1972 and 1973 (Table 15), while 5.9 such acts were observed between juveniles (from Table 16; Mann-Whitney, N.S.). Only on plot 3-1973 was adult-young cohesive behavior more frequent than that observed between young; while as many as 9.5 cohesive acts (per 100 squirrels per 45-minute period) were observed between adults and young, none were recorded among the few juveniles that were observed on that plot (Fig. 7; Mann-Whitney, N.S.).

In 1972, there was no significant difference in the intensity of juvenile cohesive behavior on the control plot (#1) and the treated plots (#2,3). Cohesive acts (per 100 squirrels per 45-minute period) averaged 6, 9 and 6 for plots 1, 2 and 3 respectively (from Table 16; Mann-Whitney tests). When intensity of interactions was compared between littermates, i.e. related juveniles, and between non-related juveniles, it appeared that no difference existed between the two groups on plot 2-1972 (8 acts among littermates versus 2 among non-related juveniles)(Table 16; Mann-Whitney, N.S.) and on plot 3 (6 versus 3; Mann-Whitney, N.S.). On the other hand, littermates from the control plot related more cohesively towards each other (7 acts) than towards non-related juveniles (1 act) (Table 16; Mann-Whitney, S.99). So although plots did not differ overall in the intensity of their juvenile cohesive behavior in 1972, interactions on the control plot were

Table 16. Average numbers of cohesive interactions observed between juvenile ground squirrels (per 45-minute observation period, per 100 squirrels).

10-day period	PLOT 1 Litt	PLOT 1 YY YLitt	PLOT 1 All young	PLOT 2 Litt	PLOT 2 YY YLitt	PLOT 2 All young	PLOT 3 Litt	PLOT 3 YY YLitt	PLOT 3 All young	PLOT 4 YY	PLOT 5 YY	PLOT 6 YY
1972												
1	-	-	-	-	-	-	-	-	-			
2	0	-	0	-	-	-	-	-	-			
3	1	2	3	0	-	0	0	-	0			
4	10	4	14	18	-	18	0	-	0			
5	15	2	17	17	5	20	21	-	21	No plots in 1972		
6	3	3	5	19	4	21	5	10	12			
7	13	0	12	8	3	10	0	2	2			
9	5	0	5	0	0	0	9	4	8			
10	0	0	0	4	1	5	0	0	0			
11	4	0	2	1	0	1	8	0	2			
10-day average	7	1	6	8	2	9	6	3	6			
1973												
0	-	-	-	-	-	-	-	-	-	NO	NO	NO
1	-	-	-	-	-	-	-	-	-	NO	NO	NO
2	-	-	-	-	-	-	-	-	-	NO	NO	NO
3	29	-	29	0	-	0	-	-	-	NO	NO	NO
4	15	-	15	17	0	13	0	-	0	NO	NO	NO
5	25	-	25	0	0	0	0	0	0	102	93	54
6	26	-	26	-	0	0	0	0	0	66	183	79
7	8	-	8			NO	0	0	0	14	13	23
8	2	-	2			NO			NO	9	36	14
9	0	-	0			NO			NO	0	0	11
11	0	0	0			NO	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	4
13	3	0	2	0	0	0	-	-	-	0	0	4
10-day average	11	0	11	3	0	2	0	0	0	24	41	24

mostly concentrated among littermates, while on the treated plots they occurred among littermates, and between juveniles that were not known to be related.

In 1973, cohesive interactions among juveniles averaged 11 acts (per 100 squirrels per 45-minute period) on plot 1 and were significantly more numerous than those observed on plots 2 (Mann-Whitney, S.95) and 3 (Mann-Whitney, S.99.5). In effect, on plot 2, only 2 such acts were recorded, while none were observed on plot 3 (Table 16). The low intensity of cohesive behavior among juveniles is attributed to their low density. The numbers of juveniles remained low throughout the summer (Fig. 7). Juvenile cohesive behavior on plots 2 (Mann-Whitney, S.99.9) and 3 (Mann-Whitney, S.99.9) was significantly less intense in 1973 than what it was in 1972; in effect, 9 and 6 cohesive acts (per 100 squirrels per 45-minute period) were observed on these plots in 1972, while only 2 and 0 were observed on these same plots in 1973 (from Table 16). On the other hand, no significant difference was observed on the control plot (#1), where averages of 6 and 11 cohesive acts were observed between juveniles in 1972 and 1973 respectively (from Table 16; Mann-Whitney, N.S.). The number of juveniles on plot 1-1973 was higher than that observed in 1972 (Fig.7).

b. Plots 4, 5 and 6

Average numbers of cohesive acts among juveniles averaged 24, 41 and 24 acts (per 100 squirrels per 45-minute period) on plots 4, 5 and 6 during 1973 (Table 16). However, they did not differ significantly from the control plot where 11 such acts were observed (Mann-Whitney, N.S.). Neither was there any difference in juvenile cohesive behavior between plots 4, 5 and 6 (Mann-Whitney test, N.S.). All three plots had significantly higher numbers of cohesive acts among juveniles than plots 2 and 3 (Mann-Whitney tests).

The timing of the peak of cohesive behavior did not differ much between plots. During both years, it was generally first observed 10 days after the first emergence of juveniles (Fig. 7), peaked 10 to 20 days later, and then steadily declined. In five plots out of 9, cohesive behavior among juveniles was observed till the end of the observations, i.e. August 12 in 1972, and August 28 in 1973 (Fig. 7). In two of the remaining plots, i.e. plots 2 and 3-1973, the absence of cohesive behavior was explained by the very low numbers of juveniles present. Thus the persistence of cohesive behavior throughout the summer seems normal for juveniles. It reaches a high intensity during a short period from 10 to 20 day after first juvenile emergence and lasts at least until 40 to 50 days afterwards.

4. Summary: cohesive behavior 1972, 1973

1. Cohesive behavior among adults was rare and occurred sporadically between mid-April and the end of June each year. More adult-adult cohesive interactions were seen on the treated plots, but no difference in intensity of interactions was observed between treated and non-treated squirrels, or between plots or years. Only neighbours and, especially related adult squirrels behaved cohesively towards each other.
2. Adult-young cohesive interactions were common. On the non-treated plots, 85% of such interactions were observed between mother and offspring, while 43% occurred between juveniles and non-related adult squirrels on the treated plots. Juveniles on treated plots received as much attention as their counterparts on the non-treated plots. Most adult-young cohesive interactions occurred in a short period, from mid-May till the end of June and corresponding to the period when the maximum numbers of ground squirrels were active on the plots. Treated adults behaved as cohesively towards juveniles as did the non-treated adult squirrels not related to the young.
3. The majority of cohesive acts (57%) occurred between juveniles. While most of them occurred among littermates on the control plot, they were also observed among non-related juveniles as well as among littermates on the two treated plots. Overall, juveniles were involved in 96% of all cohesive interactions, i.e. with other juveniles or with adult squirrels. There was no difference in cohesive interaction frequency between adult-young and young-young cohesive behavior.
4. In 1972, when all plots had normal populations of juveniles, no difference in juvenile cohesive behavior was observed between plots. In 1973, as juvenile populations on plots 2 and 3 were much reduced, cohesive behavior was less than that observed on the control plot, and also less than that observed on these same plots in 1972. Cohesive behavior among juveniles was also more intense on other non-treated plots such as plots 4, 5 and 6 than on the two treated plots.
5. Timing of juvenile cohesive behavior was roughly the same on all plots, although it ceased altogether on plots 2 and 3, when very few juveniles were present.

C. Agonistic behavior

A total of 1197 agonistic interactions were recorded on plots 1, 2 and 3 during the field seasons 1972 and 1973 (App. 4) during a total of 234 45-minute observation periods (App. 2). Similarly, 477 agonistic acts were counted on plots 4, 5 and 6 in 1973 (App. 4) during 64 observation periods (App. 2). The interactions will be analyzed here as a function of the sex and age of the squirrels involved, to indicate the effects, if any, of the mestranol treatments given. The seasonal incidence of agonistic behavior will be discussed and differences between groups of squirrels, between plots and years will be described. The nature of the agonistic interactions per se will be only briefly mentioned.

1. Adult-adult interactions

a. Plots 1, 2, 3

Comparisons between groups of adult squirrels, or between plots or years include both male and female interactions. However, a few males who were attempting to establish residence in some of the plots in 1972 accounted for a disproportionately high number of agonistic acts and consequently some comparisons are unrepresentative. Therefore, I decided to present the agonistic behavior analysis for all adult squirrels and also for adult females separately. It is likely that if the mestranol treatment had any effect upon agonistic behavior that it would show more readily among adult females. Presumably pregnancy and lactation would affect their social behavior.

i. Types of interactions

A total of 562 agonistic interactions was observed among adults on plots 1, 2 and 3 during 1972 and 1973 (App. 4), i.e. 47% of all agonistic acts recorded. The most common interaction was the chase (67%). Fights, occurring on their own (12%) or preceeded by a chase (10%) were also frequent. Less serious types of encounters such as the fight sec. (4%), fight sec. preceeded by a chase (1%), threat (3%), and face-off/avoidance (3%) were less usual (from App. 9B). Chi-square tests failed to show any difference in the frequency of types of behavior used by treated or non-treated squirrels (from App. 5 and 9B). Non-treated squirrels did not use violent forms of agonistic behavior more or less than treated squirrels. Similarly, ritualistic forms of behavior such as the threat or avoidance, etc. were not observed more frequently between treated squirrels than non-treated ones (from App. 5 and 9B).

ii. Seasonal timing

Agonistic behavior was occurring between adults when field work started on plots 1, 2 and 3 in March each year and was common when behavioral observations started (April 21, 1972; April 16, 1973). Quanstrom (1972) observed incipient agonistic behavior among adults 4 day after their emergence. Such behavior continued throughout April and May, until around mid-June each year (Fig. 7). It stopped earlier on some plots; for example, no agonistic behavior among adults was observed after the first of June on plot 3-1972. But it lasted longer in others; agonistic behavior was observed until the end of June on plot 2-1972 (Fig. 7). Interestingly, adult agonistic behavior ceased first on the least dense plot (#3) and stopped last on the highest density plot (#2). Overall, agonistic behavior among adults stopped between 10 and 30 days before onset of hibernation, and on average was terminated at least 25 days (n=9) before all squirrels hibernated (from Fig. 7). Although many adult squirrels were still present and active, they did not interact agonistically to each other after that time.

When the timing of adult agonistic behavior is compared to the calendar of biological events (Table 2), it can be seen that the period of adult agonistic behavior spans the breeding period, the establishment of home areas by females, and their pregnancy, parturition and lactation periods. Adults were still aggressive towards each other when juveniles were emerging from the maternal burrows in May (Fig. 7). However, adult agonistic behavior ceased 10 to 20 days after the last emergence of juvenile litters on each plot (from Table 2 and Figure 7). Females that had bred seemed to become less aggressive when juveniles were weaned and began to feed themselves. For example on plot 1-1972, all juveniles had emerged by the third week of May (Table 2). Juveniles were observed to be feeding on vegetation within 3 days of emergence (Quanstrom, 1971), but would still nurse for several days (Dorrance, 1974). While females were engaged in 53 agonistic acts (per 45-minute period per 100 squirrels) during the last 10 days of May, during the first 10 days of June, this was reduced to only 6 agonistic acts (Table 17). The same phenomenon was observed on all nine plots (Fig. 7) (Tables 17, 18). Levels of interactions for adult females were calculated from data summarized in Appendix 10.

iii. Agonistic behavior 1972

In 1972, the frequency of agonistic behavior between adults averaged 46, 17 and 13 agonistic acts on plots 1, 2 and 3 (Table 18). On plot 1, a large number of agonistic interactions was due to the behavior of three adult males who were trying to establish territories (Table 6, B2). However adult female interactions were still predominant, averaging 37 agonistic acts during the season (Table 17). Mann-Whitney tests showed that the level of adult agonistic behavior on the control plot (#1) was not significantly different from plot 2, but was greater than on plot 3 (App. 11, no. 5). Levels of adult aggression did not differ on plots 2 and 3 (App. 11, no. 10).

When comparisons were made between groups of squirrels, further differences emerged. While adult squirrels from plot 1, i.e. non-treated with mestranol, did not differ from non-treated squirrels from plots 2 (App. 11, no. 1), they were significantly more aggressive than mestranol treated adults from the same plot (App. 11, no. 2). Non-treated squirrels from the control plot averaged 46 agonistic acts (per 45 minute period per 100 squirrels) while only 2 such acts were observed among treated squirrels from plot 2 (Table 18). Moreover, non-treated squirrels (17 acts) from plot 2 were involved in a significantly higher number of agonistic interactions than treated squirrels (2 acts) from this same plot (App. 11 no. 2). The predominance of agonistic behavior among non-treated squirrels is clearly shown by comparing the numbers of interactions which were won by either treated or non-treated squirrels. In plot 2-1972, non-treated females were dominant in an average of 16 agonistic interactions (AA+AM), while treated females were dominant (MA+MM) in a significantly lower average of only 4 agonistic interactions (Table 17; App. 11, no. 9). Although I was unable to demonstrate a significant difference in the intensity of agonistic behavior observed among the combined adults of all types from plots 1 and 2,

Table 17. Average numbers of agonistic interactions observed for different groups of female squirrels (per 45-minute observation period, per 100 females).

10-day period	PLOT 1	PLOT 2							PLOT 3						
	AA	AA	AM	MA	MM	AA AM	MA MM	All fem.	AA	AM	MA	MM	AA AM	MA MM	All fem.
1972															
1	47	18	2	6	4	15	7	21	25	6	8	10	16	14	30
2	78	24	5	3	7	20	5	26	9	6	2	12	11	8	19
3	38	19	10	2	0	21	2	23	11	2	7	4	7	10	17
4	53	17	5	3	4	16	4	20	0	5	0	7	5	5	9
5	6	12	5	5	0	13	5	18	0	0	0	0	0	0	0
6	0	15	0	0	0	13	0	13	0	0	0	0	0	0	0
7	-	0	-	-	-	-	-	0	0	-	-	-	-	-	0
10-day average	37	15	5	3	2	16	4	17	6	3	3	6	6	6	11
1973															
0	28	10	0	4	35	7	16	23	40						
1	9	0	4	2	14	4	7	11	13						
2	18	17	0	0	12	10	5	15	15						
3	20	3	2	2	23	4	11	15	15	No mestranol treated females in 1973					
4	15	5	3	6	7	6	9	15	25						
5	15	7	0	6	0	6	6	11	16						
6	4	0	-	-	-	-	-	0	0						
7	0	NO							0						
8	0	NO							NO						
9	0	NO							NO						
10-day average	11	6	1	3	15	6	9	13	15						

Table 18. Average numbers of agonistic interactions observed for different groups of ground squirrels (per 45-minute observation period, per 100 squirrels).

10-day period	PLOT 1		PLOT 2							PLOT 3						
	AA	AY	AA	AM MA	MM	AA AM MA MM	AY	MY	AY MY	AA	AM MA	MM	AA AM MA MM	AY	MY	AY MY
1972																
1	54	–	27	7	3	26	–	–	–	25	14	11	30	–	–	–
2	84	0	24	10	6	27	–	–	–	9	16	11	26	–	–	–
3	63	3	32	10	0	29	0	0	0	11	17	4	24	4	0	2
4	66	12	25	8	3	25	3	0	2	0	4	7	9	0	0	0
5	8	21	16	8	0	19	17	0	15	0	0	0	0	0	0	0
6	0	7	17	2	0	16	16	0	15	0	0	0	0	14	0	13
7	–	–	7	–	–	7	6	0	6	0	–	–	0	3	–	3
9	–	–	0	–	–	0	1	–	1	–	–	–	–	–	–	–
10	–	–	0	–	–	0	2	–	2	–	–	–	–	–	–	–
11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10-day average	46	8 (26)* (13)**	17	8	2	17	6 (30)	0 (0)	6 (24) (12)	6	9	5	13	4 (15)	0 (0)	4 (12) (16)
1973																
0	30	–	30	9	62	52	–	–	–	51				–		
1	12	–	8	15	19	28	–	–	–	14				–		
2	18	–	18	8	10	23	–	–	–	37				–		
3	21	0	17	5	31	27	3	0	2	12				–		
4	15	1	4	24	12	32	2	0	2	30				0		
5	15	8	12	4	0	14	8	0	7	36				5		
6	4	27	0	–	–	0	0	–	0	0				0		
7	0	10			NO					0				0		
8	0	2			NO									NO		
9	0	0			NO									NO		
11	–	–			NO					0				0		
12	–	–	–	–	–	–	–	–	–	–				–		
13	–	–	–	–	–	–	–	–	–	–				–		
10-day average	10	7 (34)* (9)**	13	11	22	25	3 (4)	0 (0)	2 (3) (5)	23				1 (1.4) (3)		

( )* : average number of adult-young interactions per adult only
( )** : average number of adult-young interactions per young only

there was no doubt that non-treated squirrels from these two plots were more aggressive than treated squirrels from plot 2.

However, the mestranol treatment is not the only factor to be taken into consideration. On plot 3-1972, there was no significant difference in the agonistic behavior of treated and non-treated squirrels. Interactions dominated by treated females (MA+MM) and by non-treated females (AA+AM) both averaged 6 agonistic acts (Table 17; App. 11, no. 9). Non-treated squirrels from the control plot were more aggressive than both treated and non-treated squirrels from plot 3 (App. 11, no. 1, 2, 3, 4, 5). Overall, there was no difference between the intensity of the agonistic behavior of all squirrels (treated and non-treated) from plots 2 and 3 (App. 11, no. 10). However, non-treated females from plot 2 were more aggressive than both non-treated (App. 11, no. 1) and treated (App. 11, no. 2) females from plot 3. Treated females from both plots did not differ significantly in agonistic behavior (App. 11, no. 7).

Non-treated squirrels from plots 1 and 2 were thus consistently more aggressive than treated squirrels whether they came from plot 2 or 3. Non-treated squirrels from plots 1 and 2 were also more aggressive than similarly non-treated squirrels from plot 3 while no differences were found between plots 1 and 2 for these two groups (App. 11, no. 1). I attribute the difference in the levels of agonistic behavior for non-treated squirrels between plots 1, 2 and 3 to differences in population density. Plots 1 and 2 had comparable densities of active adult squirrels throughout the 1972 summer as averages of 18.2 and 15.1 adult squirrels were observed above ground (Table 19; Mann-Whitney test, N.S.). Plot 3 had an adult density of 8.6 squirrels that was significantly lower than those observed on plots 1 (Table 19; Mann-Whitney, S.95) and 2 (Mann-Whitney, S.95). This lower density seemed to reduce the levels of agonistic behavior observed on plot 3.

The levels of agonistic behavior observed on plots 2 and 3 may have been reduced because mestranol treatment affected the overall level of activity of treated squirrels. I have shown (Section I.A) that mestranol given in April 1972 effectively sterilized all but one of the treated females. It is possible that such females, not having to undergo pregnancy and lactation, would have been less active than their breeding counterparts.

Table 19. Average densities of active ground squirrels observed during a 45-minute observation period on plots 1, 2 and 3 during 1972 and 1973.

10-day	1972						1973					
	PLOT 1		PLOT 2		PLOT 3		PLOT 1		PLOT 2		PLOT 3	
period	A	Y	AM	Y	AM	Y	A	Y	AM	Y	A	Y
0							38.0	-	26.0	-	18.5	-
1	29.2	-	23.4	-	11.8	-	33.8	-	27.9	-	14.8	-
2	22.8	1.2	22.6	-	12.4	-	30.0	-	23.2	-	9.9	-
3	15.8	22.3	20.0	4.3	10.1	1.2	27.4	22.6	22.4	0.3	9.9	-
4	21.6	28.9	24.7	14.2	10.8	2.2	10.3	44.1	19.7	11.0	8.3	1.6
5	11.7	25.5	21.0	29.9	7.4	5.9	10.0	36.2	15.9	5.8	8.6	3.7
6	7.4	23.7	14.1	31.0	5.0	10.2	18.5	53.8	11.6	5.8	2.5	3.7
7	-	29.7	6.8	34.8	2.8	12.7	8.2	45.1	NO		2.5	7.4
8	NO		NO		NO		3.1	45.1	NO		NO	
9	-	26.6	2.5	23.2	-	13.0	3.1	34.6	NO		NO	
10	-	24.9	1.2	31.6	-	16.0	NO		NO		NO	
11	-	24.3	-	30.4	-	10.6	-	23.6	NO		-	7.4
12							-	22.6	-	8.7	-	3.7
13							-	21.6	-	4.3	-	-
10-day average	18.2	23.0	15.1	24.9	8.6	9.0	18.2	34.9	20.9	6.0	8.4	4.6

As they may not have had to feed as much, they would have been seen above ground less often. To check this idea, I have defined a measure of squirrel activity as the proportion (%) of 45-minute observation periods during which a given squirrel was observed above ground between the start of behavioral observations and the return of this squirrel into hibernation. Such data is summarized in Appendix 12. When individual data is summarized for 24 adult resident females in 1972, chi-square tests showed no significant differences in the activity levels of treated and non-treated squirrels. While non-treated squirrels from plots 1, 2 and 3 were active during 81%, 85% and 79% of the observation periods, mestranol treated squirrels from plots 2 and 3 were observed during 78% and 76% of the observation periods (App. 12). No difference could be shown between these groups when plots 1, 2 and 3 were compared; neither was there any significant differences in levels of squirrel activity when the treated and non-treated squirrels from plot 2 were compared (Chi-square, N.S.).

The differences observed in levels of agonistic behavior on plots 1, 2 and 3 in 1972 could thus be attributed to differences in the adult population density and the mestranol treatment given. No difference in activity could be shown for treated squirrels.

iv. Agonistic behavior 1973

In 1973, agonistic acts among adults averaged 10, 25 and 23 interactions (per 45-minute per 100 squirrels) on plots 1, 2 and 3 respectively (Table 18). No significant differences were found between the plots when numbers of agonistic acts were compared for all squirrels combined (Table 18) or for adult females only (Table 17) (App. 11, no. 5).

As was the case in 1972, the intensity of agonistic behavior on plot 2 did not differ from the control plot (#1) in 1973 (App. 11, no. 5), and groups of non-treated squirrels had indistinguishable levels of agonistic behavior on both plots (App. 11, no. 1). However, contrary to 1972, no difference was found between the non-treated females from plot 1 and the treated females from plot 2 (App. 11, no. 2). Moreover, no difference was found between groups of treated and non-treated squirrels within plot 2 itself (App. 11, no. 2). Interactions dominated by non-treated females (AA+AM) and by treated females (MA+MM), respectively averaged 6 and 9 agonistic acts (Table 17) and were not significantly different (App. 11, no. 9). Thus in 1973, treated squirrels were not statistically less agonistic than their non-treated counterparts.

There was no significant difference in the levels of agonistic behavior shown by the adult squirrels found on plots 1 and 3 during 1973. Non-treated females from the control plot (#1-1973) interacted on an average of 11 times throughout the season, while similarly non-treated females from plot 3 were involved in 15 interactions (Table 17; App. 11, no. 1). No difference could be shown when all squirrels were considered (Table 18; App. 11, no. 1).

In 1973, plots 1 (18.2) and 2 (20.9) had equal densities of active adults (Table 19; Mann-Whitney, N.S.), and their numbers of residents (14 and 16) were roughly the same (Table 6). However, 81% of the squirrels resident on plot 2 were affected by a previous mestranol treatment while none were on plot 1 (Section III.C.2.c). Yet no difference in the agonistic behavior of the adults was seen between these two plots. Plot 3 was not treated in 1973 (Table 1), but had a significantly lower density of active adults (9.4) than plot 1 (18.2; Mann-Whitney, S.95) and plot 2 (20.9; Mann-Whitney, S.95) (Table 19). In spite of these differences in treatment or density between plots 1, 2 and 3, differences in the levels of agonistic behavior of their adult populations could not be demonstrated on the basis of the observations made.

Levels of adult agonistic behavior did not differ on the three plots when 1972 was compared with 1973. On plot 1, adult females interacted agonistically on an average of 37 occasions during 1972 while they were observed in only 11 such encounters in 1973 (Table 17). No significant difference could be shown between the years (App. 11, no. 1). No differences were seen either when levels of agonistic behavior were compared between the 1972 and 1973 seasons on plot 2 (App. 11, no. 10) and plot 3 (App. 11, no. 13).

However, when levels of agonistic behavior were compared between 1972 and 1973 for the 10-day periods 1 to 4 only, i.e. late April to late May during which time pregnant females were actively establishing and defending home areas, a difference was shown on the control plot. During that period in 1972, level of adult agonistic behavior was greater than observed in 1973 (from Tables 17 and 18; Mann-Whitney, S.99.9). However, such a difference could not be shown for the same period on plots 2 and 3.

On plot 1, no mestranol treatments were given in 1972 and 1973 (Table 1). Each year densities of active squirrels (18.2 squirrels per 45-minute period, per hectare) were the same (Table 19; Mann-Whitney, N.S.), although more squirrels were resident in 1973 (14) than in 1972 (10) (Table 6). Still no overrall change was seen in the behavior of adult squirrels between 1972 and 1973, and in fact, frequency of agonistic behavior decreased in May 1973 in spite of a higher resident density. On plot 2, treatment was increased in 1973 (81%; Section III.C.2.c) as compared to 1972 (53%; Table 1)). Densities of active squirrels did not differ significantly on that plot in both years (15.1 versus 20.9) (Table 19; Mann-Whitney, N.S.), although fewer adults were resident in 1973 (16 versus 21 in 1972; Table 6). Still, adult agonistic behavior was not reduced as a result of the decreased number of residents and greater impact of the mestranol treatment in 1973. On plot 3, no treatment was given in 1973, as opposed to a 78% treatment in 1972 (Table 1). The same number of squirrels were resident (10) each year (Table 6), and the densities of active adults were the same in 1972 (8.6) as in 1973 (9.4) (Table 19; Mann-Whitney, N.S.). However, the absence of mestranol treatment in 1973 did not bring an increase of agonistic behavior.

This lack of difference between plots in 1973, and within plots for 1972 and 1973 was not attributable to a change in the levels of squirrel activity. Adult squirrel activity in 1973 was the same on plots 1, 2 and 3 (Chi-square, N.S.), as it averaged 73%, 87% and 87% on each plot respectively (App. 12). There was no difference in activity between treated and non-treated squirrels from plots 2 (Chi-square, N.S.) as those groups were active during 93% and 81% of their respective observation periods (App. 12). No differences were shown, for any plot or for all plots pooled together, between the levels of activity observed in 1972 and in 1973; squirrels were as active in 1973 as they were in 1972 (Chi-square, N.S.). Similarly, no differences were shown between the 1972 and 1973 seasons when groups of treated and non-treated squirrels were compared (Chi-square, N.S.).

The fact that levels of agonistic behavior were the same on all plots in 1973 was inconsistent with the relationships observed in 1972. i.e. aggression is reduced on treated plots and on plots of low density. Therefore I will consider other factors to possibly explain these discrepancies. The spatial distribution of the squirrels on the plots will be described for 1972 and 1973, and comparisons will be made between plots and between years.

v. Spatial distribution 1972, 1973

The spacing of animals in their habitat has been shown to be related to their aggressive tendencies as well as to their need for a necessary food supply or breeding site (Brown, 1964). This is why the spatial distribution of the squirrel populations observed in 1972 and 1973 will be analyzed here to establish possible relationships between treatment, social behavior and physical distribution of the squirrels on the plots.

Yeaton (1969) described the area defended by Richardson's ground squirrels as being territories. However, the term 'territory' has been defined in many ways (Nice, 1953; Burt, 1949; Wilson, 1971; and others). Many describe it as 'any defended area' (Noble, 1939), while others consider it to be 'any area used exclusively by one or more animals' (Pitelka, 1959). Some researchers (Quanstrom, 1971; Yeaton, 1972; Wehrell, 1973) consider the Richardson's ground squirrel to be a 'territorial' species having more or less exclusive use of its territory. However, Michener (1979) states that no territory is actively defended by this species and that rather, females are less submissive towards other squirrels in their own 'core area' than away from it. In this study, the words 'territories' or 'home areas' refer to the areas taken over by squirrels when they establish residency in the spring; social status is discussed in terms of 'residents' versus 'non-residents'.

Spatial distribution is quantified in terms of 'core area'. The 'core area' was first defined by Kaufmann (1962), and as used by Michener (1979) represents 'the area in which a squirrel concentrated 50% of its above ground time'. The core area in the present study covers 50% of all points where a squirrel was observed on the plot. This area, radiating from the home burrow, is the one mostly used by squirrels during the periods of breeding, pregnancy and lactation. After juvenile emergence, adult females extend their home range. Although data was not collected as accurately as by Michener (1979), a reasonable approximation of the core area size was obtained (Materials and Methods) as sample sizes were large. The spatial configuration of core areas is given for all adults residing on plots 1, 2 and 3 during 1972 and 1973 (Fig. 8) and estimates of their sizes are summarized for 66 resident adult squirrels (Table 20; App. 13).

v.1. Area core size

In 1972, core areas measured for all squirrels on plots 1, 2 and 3 respectively averaged 288 m2, 233 m2 and 346 m2 (Table 20). No significant difference in core area size was found between the control plot (#1-1972) and the two treated plots (Mann-Whitney, N.S.), but the average core area on plot 3 was greater than on plot 2 (Mann-Whitney, S.95). In 1973, core areas for all squirrels respectively averaged 231 m2, 231 m2 and 406 m2 in these same plots (Table 20). In 1973, plot 3 core areas were larger than those observed on plot 1 (Mann-Whitney, S.99) and plot 2 (Mann-Whitney, S.99), while the average core areas from plots 1 and 2 were not different (Mann-Whitney, N.S.).

This data seems to indicate that no relationship existed between the size of the core areas measured in the different plots and the mestranol treatment they had received. If such was the case, a difference would have existed between the control plot and both of the treated plots. Rather, the size of the core areas seemed to be more directly related to the adult resident densities observed on these plots. In 1972, the largest area cores were observed in the least dense plot (3#), while the densest plot (#2) (30.4 resident per hectare as opposed to only 12.3 on plot 3) had the smallest core areas (Tables 5 and 20). In 1973, plot 3 was again the least dense plot (12.3 residents per hectare) (Table 5) and showed significantly greater core areas than plots 1 and 2. The latter plots had comparable resident densities (21.6 and 23.2 residents per hectare), and also have same size core areas (Table 5; Table 20). Thus there seems to be a direct relationship between resident adult densities and size of core areas used. Figure 9, relating core area size and corresponding resident densities, seems to indicate three types of relationships. At squirrel densities below 13 per hectare, the size of core area does not seem to be limited by any social factors. Between densities of 13 to 22 squirrels per hectare, an

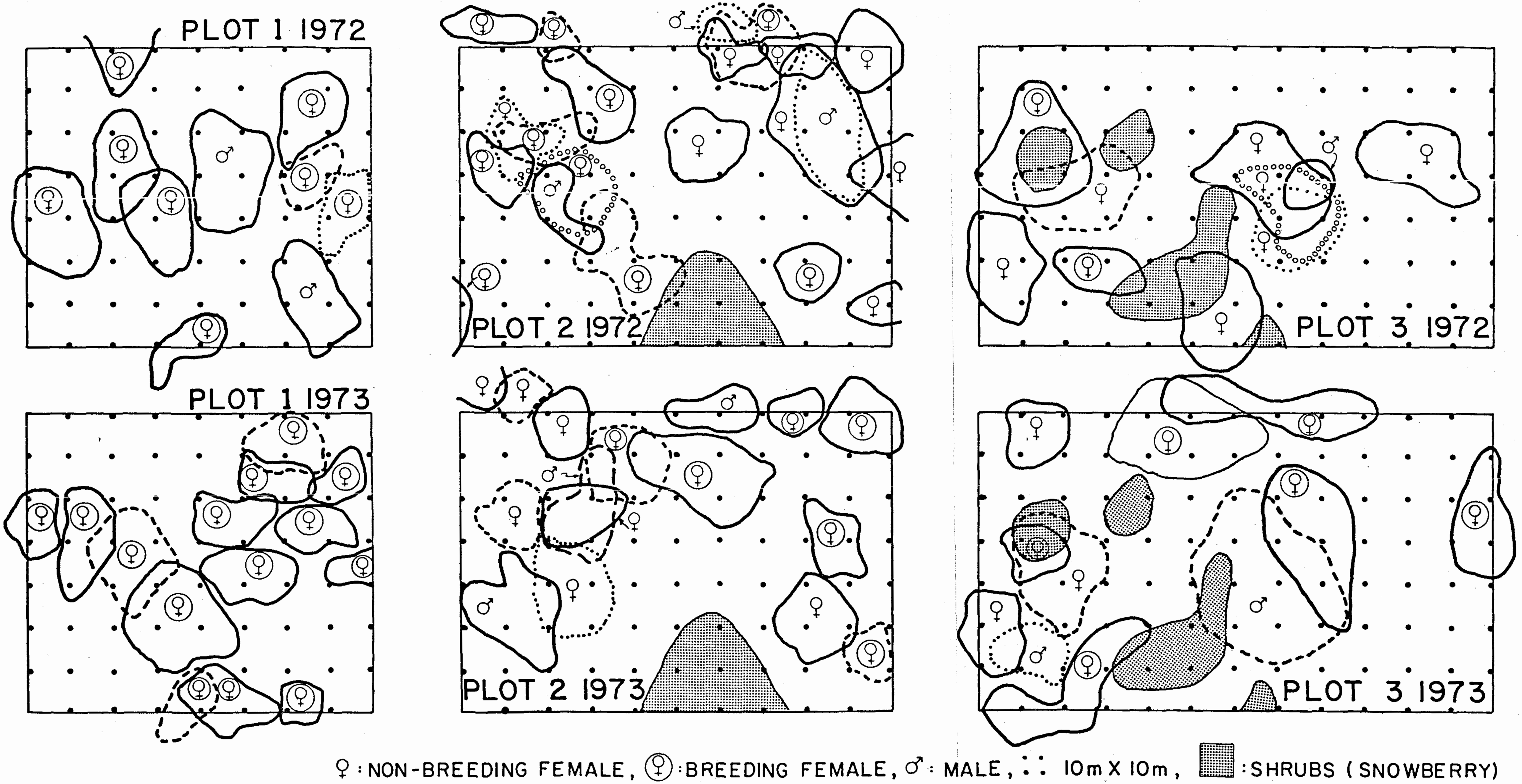


Figure 8. Maps of resident adult core areas as observed in the ground squirrel populations found on plots 1, 2 and 3 during the field seasons 1972 and 1973.

Table 20. Average size of individual core areas and home ranges for different categories of adult ground squirrels residing on plots 1, 2 and 3 during 1972 and 1973.

	Average area (m2± S.D.) including a given percentage of all points where a squirrel was observed within a given plot							
			1972				1973	
Percentage of points included in area	n	Core area 50%	75% Area 75%	Home range 95%-100%	n	Core area 50%	75% Area 75%	Home range 95%-100%
PLOT 1								
Breeding females	7	273± 75	456±144	855±192	13	231± 104	459± 252	887± 466
Males	2	343±110	565± 7	1032± 81	0	-	-	-
All squirrels	9	288± 82	480±133	894±186	13	231±104	459± 252	887± 466
PLOT 2								
Breeding females	8	220± 75	419±103	922±391	6	245±144	498± 330	818± 543
Non-breeding females	6	262±169	507±325	1098±621	6	213± 73	443± 197	912± 261
Males	1	170	280	950	2	240± 99	500± 311	935± 658
All squirrels	15	233±117	445±217	995±472	14	231±105	475± 255	875± 419
PLOT 3								
Breeding females	2	315±205	610± 0	1365±318	5	432±156	856± 295	1620± 345
Non-breeding females	6	357± 84	523± 74	1242±366	2	345±205	710± 424	1100± 750
Males	0	-	-	-	0	-	-	-
All squirrels	8	346±107	545± 74	1272±337	7	407±158	814± 305	1471± 487
ALL PLOTS								
Breeding females	17	253± 92	456±127	947±336	24	276±145	551± 312	1022± 545
Non-breeding females	12	309±137	515±225	1170±492	8	246±116	510± 262	959± 370
Males	3	285±126	470±165	1005± 75	3	513±479	1163±1170	1740±1470
All squirrels	32	277±113	480±169	1036±395	34	267±134	539± 293	1002± 500

n: sample size

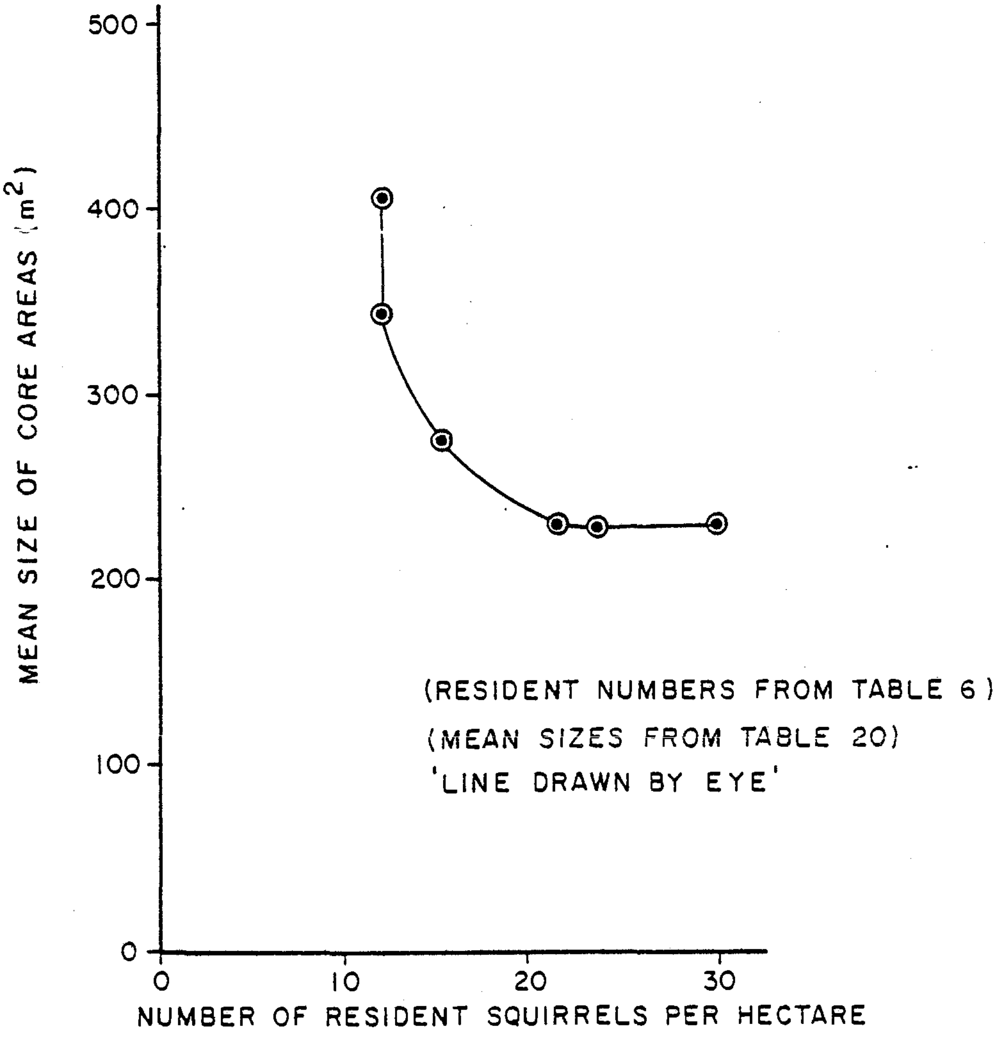


Figure 9. Relationship between the density of resident adult squirrel populations and the average sizes of the core areas utilized by these squirrels.

inversely proportional relationship exists between density and size of core area; the more squirrels there are, the smaller the core areas. Finally, above a density of 22 squirrels per hectare, core area size remains constant; thus 230 m2 is probably the minimum core area needed by a squirrel to sustain itself.

In 1972, breeding females from plots 1, 2 and 3 on average used a 253 m2 core area, while non-breeding females used a 309 m2 core area of comparable size (Table 20; Mann-Whitney, N.S.). In 1973, breeding and non-breeding females did not differ either as they used 276 m2 and 246 m2 core areas, respectively (Table 20; Mann-Whitney, N.S.). Similarly, no differences were found when groups of breeding and non-breeding females were compared within plots 2 and 3 during the 1972 and 1973 seasons (Table 20; Mann-Whitney, N.S.). Males did not differ from either breeding or non-breeding females when core areas were compared within or between plots in 1972 and 1973 (Table 20; Mann-Whitney, N.S.). In this latter case though, it is not known if the lack of difference is real or is rather due to the small sample size available for male core areas. It was shown by Michener (1968) that adult males and females have same size home ranges. It would seem certain that the size of the core area is not related to the breeding status of the ground squirrels as no difference could be shown between breeding and non-breeding females. This also explains the lack of difference observed between treated and non-treated plots.

In 1972, core areas for all squirrels in all plots averaged 277 m2, and did not differ significantly from the 267 m2 core areas observed in 1973 (Table 20; Mann-Whitney, N.S.). No difference could be shown in the size of core areas when 1972 and 1973 data were compared for any of the plots. On the control plot (#1), no difference could be demonstrated between the 288 m2 and 231 m2 core areas observed on this plot in 1972 and 1973 respectively (Table 20; Mann-Whitney, N.S.). It should be remembered that in 1973, more squirrels were resident on plot 1 than in 1972 (Table 6). This means that in 1973, either the total area used by squirrels within the plot was extended, or else core area overlap was greater. Core area overlap and total area used by squirrels within each plot will now be presented and compared to check such an eventuality.

v.2. Core area overlap and total core area

The total area used by the resident squirrels was calculated for plots 1, 2 and 3 in 1972 and 1973; this was defined by the outside boundaries of all core areas occupied by the different squirrels. For example in plot 1-1972, all resident squirrel core areas occupied a total space of 2640 m2; since the plot itself covered 6400 m2, 3760 m2 were not included in the core areas (Fig. 8; Table 21). The remainder of the plot not included in the core area distribution is ignored here; only ground covered by core areas is considered in the calculations.

Overlap is defined as the percentage of the total core area space where two or more individual core areas overlapped. All core areas shown in Figure 8 were used to calculate the total area occupied by resident squirrels on the three plots in 1972 and 1973. Overlap areas were calculated and the respective percentage they represented in each plot are summarized in Table 21. Also the total area and the overlap area were divided by the number of resident squirrels to compare the space exclusive to each squirrel, and the space each resident had to share with one or more squirrels.

In 1972, resident squirrels from the treated plots, i.e. plot 2 (Chi-square, S.99.9) and plot 3 (Chi-square, S.99.9), shared a significantly greater proportion of the total core area space than did squirrels on the control plot (#1-1972). Squirrels from plot 1 shared only 2% of the total core areas, which is negligible given the accuracy with which the core areas were measured, while squirrels from plots 2 and 3 respectively shared 37% and 18% of the occupied space (Table 21). Overlap was significantly greater on plot 2 than on plot 3 (Chi-square, S.99.9).

Amount of overlap seemed to be a result both of the mestranol treatment and of the adult densities of the plots. Plot 3 , a less dense but treated plot, had greater overlap than a high density non-treated plot (#1). Individual squirrels on both of these plots had as much space available to them, i.e. 264 m2 and 259 m2 on plots 1 and 3 respectively; but squirrels from plot 3 apparently chose to share more of it, i.e. an average of 48 m2 on plot 3 as opposed to only 5 m2 on plot 1 (Table 21). This difference between plots 1 and 3 was seen as a result of a low intensity of agonistic behavior resulting from low densities and the

Table 21. Total areas occupied by resident adult squirrels - as determined by the outline of core areas (from Figure 8) in plots 1, 2 and 3 during 1972 and 1973; average portions of the area available, exclusive and shared by each squirrel.

	1972			1973		
	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
A. Total area occupied by all squirrels (m2)	2640	2995	2590	2885	3225	3905
B. Overlap area shared by two or more squirrels (m2)	50	1105	480	160	430	420
Percentage overlap (B/A) x 100	2%	3%	1%	5%	1%	11%
Number of squirrels	10	18*	10	14	16	10
Average portion of the area (m2):						
- available to each squirrel	264	166	259	206	201	390
- shared with one or more squirrels	5	61	48	11	26	42
-exclusive to each squirrel	259	105	211	195	175	348

*: Not all resident area cores were used here as three of them were located at the edge of the plot and could not be accurately measured.

mestranol treatment. However, the fact that more overlap was found on plot 2 than on plot 3 indicates that higher density in a treated plot (#2) resulted in greater overlapping of core areas (Table 21). This greater sharing observed on plot 2 was most likely the result of 1. the reduced levels of agonistic behavior and 2. the limited size of areas within the plot offering adequate food supply. The first factor, i.e. social tolerance, allowed more squirrels than expected to share a given food supply. This is illustrated by the higher resident density observed on this plot (Table 5). Inspection of distribution of individual squirrel core areas within plots 2 and 3 (Fig. 8) shows that the core area sharing was almost exclusively between treated squirrels and other treated squirrels, or between treated and non-treated squirrels.

Squirrels in 1973 shared 5%, 13% and 11% of the total area covered by core areas on plots 1, 2 and 3 respectively (Table 21). While overlap was significantly greater on both plot 2 (Chi-square, S.99.9) and plot 3 (Chi-square, S.99.9) than on plot 1, it did not differ between plots 2 and 3 (Chi-square, N.S.). The differences between plots 2 and 3 and the control plot were attributed to the fact that both plots were seen to be equivalent to almost totally treated plots; the proportion of females breeding on these plots was very low (Table 7). The fact that overlap on plot 2-1973 was not greater than observed on plot 3, apparently resulted from the reduction in the number of resident adults on plot 2-1973 (Table 6); fewer squirrels were resident on plot 2, so that overlap was also reduced. Again the amount of overlap was both a function of the resident density, and of the breeding status of the squirrels.

When percentages of overlap are compared between 1972 and 1973, it appears that overlap on plot 1 was greater in 1973 than in 1972 (Chi-square, S.99.9), was smaller on plot 2-1973 than on plot 2-1972 (Chi-square, S.99.9), and was also smaller on plot 3-1973 than on plot 3-1972 (Chi-square, S.99). The increase in overlap on plot 1 can easily be explained by the increase in the number of residents on that plot in 1973. Similarly, the decrease of residents on plot 2 was followed by a decrease in core area overlap. However, on plot 3, the number of residents was the same each year (Table 6). The decrease in overlap could be explained by the fact that plot 3 was not treated in 1973. It was shown in 1972, that overlap was less on non-treated plots.

However, another factor may be involved as well. It was observed that in 1973, total core area space had increased on all plots when compared to 1972 (Table 21). While all area cores covered 2640 m2, 2995 m2 and 2590 m2 on plots 1, 2 and 3 in 1972, they covered 2885 m2, 3225 m2 and 3905 m2 on these same plots in 1973 (Table 21). The increases in total core areas represented 8%, 7% and 34% of the total area used by squirrels from plots 1, 2 and 3 in 1973 (from Table 21). This increase in total area used is thought to result directly from the better vegetation conditions observed in 1973. As it was shown previously, vegetation was lusher in 1973 than in 1972 (Fig. 2A and 2B). It is likely that areas that were marginal in 1972 could support squirrel populations in 1973, allowing squirrels to spread themselves if not constricted by higher resident densities. It is noticable that the greatest increase occurred on plot 3, the most marginal and least dense plot. Plots 1 and 2 which had comparable densities in 1972 also had a comparable increase in used area (Chi-square, N.S.). Both plot 1 (Mann-Whitney, S.95) and plot 2 (Mann-Whitney, S.99.5) were denser than plot 3 in 1972 (Table 19). Conversely, the increase in the total area covered by core areas was greater on plot 3-1973 than on plot 1-1973 (Chi-square, S.99.9) and plot 2-1973 (Chi-square, S.99.9).

b. Plots (1), 4, 5 and 6

Numbers and densities of all squirrels trapped, densities of active squirrels per observation period and average numbers of agonistic interactions per observation period will be compared to determine if the squirrel populations on these plots interacted similarly to those populations previously discussed.

Five, four and eight adults were trapped on plots 4, 5 and 6 in early June 1973, giving densities of 12.5, 10.0 and 20.0 adult squirrels on these plots; fourteen adult squirrels were resident then on plot 1 for a density of 21 squirrels per hectare (Table 22). Knowing the annual cycle of the Richardson's ground squirrel in the area, I feel it is safe to assume that the squirrels observed on plots 4, 5 and 6 were also residents. Plots 1 and 6 had roughly equivalent densities, while plots 4 and 5 had smaller numbers than plots 1 and 6. Plots 4 and 5 were comparable in density.

Table 22. Numbers and densities of adult and juvenile squirrels trapped or known to be resident on plots 1, 4, 5 and 6 during the months of June, July and August 1973.

MONTH OF OBSERVATION	PLOT 1 (0.65 ha)			PLOT 4 (0.40 ha)			PLOT 5 (0.40 ha)			PLOT 6 (0.40 ha)		
	A	A+Y	Y	A	A+Y	Y	A	A+Y	Y	A	A+Y	Y
	NUMBERS OF SQUIRRELS PRESENT											
June	14	68	54	5	22	17	4	19	15	8	33	25
July	3	32	29	1	16	15	2	14	12	4	25	21
August	-		21	-		8	-		9	-		13
	DENSITIES OF SQUIRRELS PRESENT (squirrels per hectare)											
June	21.5	104.6	83.1	12.5	55.0	42.5	10.0	47.5	37.5	20.0	82.5	62.5
July	4.6	49.2	44.6	2.5	40.0	37.5	5.0	35.0	30.0	10.0	62.5	52.5
August	-	-	32.3	-	-	20.0	-	-	22.5	-	-	32.5

On average, 8.6, 2.5, 4.2 and 9.0 adults were active on plots 1, 4, 5 and 6 during a 45-minute period through the 1973 summer (Table 23). Since these were the individuals available for behavioral observations, the active squirrel densities are used as the basis for comparing levels of agonistic behavior. Mann-Whitney rank tests were used to compare the densities of active adults on all the plots, and generally no significant difference existed in the numbers of active adults with the exception of plot 6 which had a greater number of active squirrels than plot 4 (App. 14, no. 1).

During the period of June 1 - August 28, 1973, averages of 4, 65, 24 and 30 agonistic interactions were observed among the adult squirrels of plots 1, 4, 5 and 6 (Table 24). Levels of aggression seemed greater on the three 0.4 hectare plots than on the control plot. However, large fluctuations of agonistic behavior from a 10-day period to another on the latter plots increased variability and when compared with Mann-Whitney ranking tests, levels of agonistic interactions among adults were not different on any of the plots (App. 14, no. 4).

No differences could be shown in the levels of agonistic behavior observed among adults of plots 1, 4, 5 and 6, although generally the counts indicated that there was more aggression on the three 0.40 hectare plots. No difference could be shown between densities of active adult squirrels on these plots, except that plot 6 which had a greater density than plot 4.

Table 23. Densities of adult and juvenile squirrels active on plots 1, 4, 5 and 6 during the months of June, July and August 1973.

10-DAY	DENSITIES OF DIFFERENT GROUPS OF SQUIRRELS (squirrels per 45-minute)											
	PLOT 1			PLOT 4			PLOT 5			PLOT 6		
PERIOD	A	A+Y	Y	A	A+Y	Y	A	A+Y	Y	A	A+Y	Y
5	10.0	46.2	36.2	4.5	33.7	29.2	9.2	35.9	26.7	13.2	47.7	34.5
6	18.5	72.3	53.8	4.5	15.7	11.2	7.5	15.0	7.5	11.2	41.2	30.0
7	8.2	53.3	45.1	0.5	30.0	29.5	0.2	43.5	43.2	8.5	33.7	25.2
8	3.1	48.2	45.1	0.5	34.7	34.2	2.7	32.4	29.7	7.5	37.7	30.2
9	3.1	37.7	34.6	-	-	30.5	1.5	25.2	23.7	4.5	39.0	34.5
11	-	-	23.6	-	-	18.7	-	-	22.0	-	-	25.7
12	-	-	22.6	-	-	14.0	-	-	19.5	-	-	27.7
13	-	-	21.6	-	-	14.0	-	-	15.7	-	-	18.2
10-day average	8.6	51.5	35.3	2.5	28.5	22.7	4.2	30.4	23.5	9.0	39.0	28.2

Table 24. Levels of agonistic behavior observed among different groups of squirrels on plots 1, 4, 5 and 6 during the months of June, July and August 1973.

10-day	NUMBERS OF AGONISTIC INTERACTIONS (per 45-minute per 100 squirrels)											
	PLOT 1			PLOT 4			PLOT 5			PLOT 6		
period	AA	AY	YY	AA	AY	YY	AA	AY	YY	AA	AY	YY
5	15	8	4	111	30	47	54	21	47	85	34	33
6	4	27	50	0	8	422	66	142	283	67	67	46
7	0	10	39	150	2	90	0	2	58	0	54	69
8	0	2	28	0	0	41	0	18	70	0	13	41
9	0	0	13	-	-	37	0	10	110	0	13	40
11	-	-	13	-	-	9	-	-	19	-	-	82
12	-	-	23	-	-	42	-	-	17	-	-	40
13	-	-	0	-	-	6	-	-	26	-	-	27
10-day average	4	9	21	65	10	87	24	39	79	30	36	47

c. Summary: Adult-adult agonistic behavior

1. Agonistic behavior was common among adults on all plots during the 1972 and 1973 seasons (47% of all agonistic acts) and treated and non-treated squirrels did not differ as to their types of agonistic interactions.
2. Agonistic behavior among adults was observed from late March until early June each year and was at its maximum when adult females were busy establishing and maintaining territories. Cessation of agonistic behavior among adults preceeded their return into hibernation by an average of 25 days.
3. The activity of adult squirrels was not affected by the mestranol treatment as treated squirrels were active above ground as often as non-treated squirrels.
4. In 1972, levels of agonistic interactions observed on plots 1, 2 and 3 showed that agonistic behavior between squirrels was affected by factors of density and breeding status. Treated squirrels were less agonistic than non-treated squirrels, and non-treated squirrels from low density plots were less agonistic than non-treated squirrels from high density plots. For treated squirrels, agonistic behavior did not change with density.
5. The densities of active adults were generally similar on plots 1, 4, 5 and 6 during the period of June 1 - August 28, 1973. The levels of agonistic interactions among these adults did not differ between the plots, although there was indication that they may have been higher on plots 4, 5 and 6.
6. Evidence gathered during the 1973 season on plots 1, 2 and 3 indicated that adult density and the spatial distribution of the resident populations were related. Core area size changed with density; less dense plots were characterized by larger core areas. Moreover, overlap of core areas was greater in denser plots (with equal treatment, or no treatment at all).
7. Treatment, i.e. breeding status, also influenced the spatial distribution of the resident populations. Size of core area did not differ for treated and non-treated squirrels, but core area overlap increased with treatment. The adults responsible for this situation were mostly treated squirrels. In effect, the latter shared their core

areas with treated and non-treated squirrels, while overlap of core areas among non-treated adults was far less common.

8. Spatial distribution of the squirrels may also have been influenced by the weather and the resultant vegetation conditions. Lusher vegetation was observed in 1973, concurrently with an increase of the total area used by squirrels within a given plot. If resident density remained the same between 1972 and 1973, core area overlap decreased as squirrels were free to occupy a larger area (plot 3). If resident density increased concurrently with the better vegetation conditions and that total area occupied did not increase much, increased overlap occurred while agonistic behavior remained the same (plot 1).

2. Adult-young interactions

a. Plots 1, 2 and 3

i. Types of interactions

A total of 175 agonistic interactions was observed between juveniles and adults on plots 1, 2 and 3 during 1972 and 1973, representing 15% of the 1197 agonistic acts recorded (App. 4) during 234 45-minute observation periods (App. 2).

The most frequent type of agonistic interaction observed between adults and juveniles was the chase (60%). Fights were not uncommon, occurring either on their own (10%) or combined with a chase (7%). The bite (10%), an agonistic interaction peculiar to adult-young relationships, was common and was also observed in combination with chases (5%). Finally the fight sec., on its own (2%) or preceded by a chase (1%), the threat (5%) and the face-off/avoidance (1%) were not observed frequently (App. 9B).

Of the 175 agonistic interactions , only one involved aggression between a female and her offspring (App. 4). This occurred on plot 2-1972, where a female started chasing its own young from a distance, perhaps mistaking it for a foreign juvenile. She stopped pursuit as soon as she came into its proximity. Otherwise, all other adult-young agonistic interactions took place between juveniles and adult squirrels that were not related.

Twenty-six (15%) of the 175 adult-young agonistic interactions were won by juveniles (App. 4); all these took place between June and mid-July (period 5-10). At that time, adult squirrels were actively preparing for hibernation (Table 2). Most of these encounters, i.e. 19 out of 26, took place between a resident juvenile and a transient adult squirrel going through the plot. Only six were observed between a resident juvenile and a resident adult. These 26 interactions are included in the summation of adult-young agonistic interactions so that data in tables and appendices include all adult-young interactions, regardless of which squirrels won the interaction.

ii. Seasonal timing

Agonistic interactions between adults and juveniles started very soon after the emergence of the latter from the maternal burrow. On plot 2-1973 and 3-1972, adult-young agonistic acts were observed during the same 10-day period that saw the first emergence of juveniles (Fig. 7); on all other plots, adult-young aggression was first observed during the 10-day period immediately following the first juvenile emergence period (Fig. 7).

Agonistic behavior between adults and juveniles first started at low levels averaging only 1.4 agonistic acts per 45-minute period (n=6) for the 3 plots during the first two 10-day periods of its occurrence (from Table 18). It reached a peak roughly a month after first juvenile emergence, averaging then 13 agonistic acts per 45-minute (n=6) on the three plots in 1972 and 1973 (from Table 18). Finally interactions diminished, and ceased on average 14 days (n=7) before the return of all adults into hibernation (from Fig. 7). Although adult and juvenile squirrels were all present on the plots for at least two weeks before the dissappearance of the adults, they no longer reacted aggressively to each other.

iii. Frequency 1972

It was shown in the Materials and Methods Section that average number of social interactions was obtained by dividing the total number of interactions, for example between adults and young, by the average number of squirrels involved; in this case, adults and young. This method of calculus is based on the reasoning that the probability of interaction between two groups of squirrels is a function of the combined numbers of these two groups. The social interaction data presented in all tables is based on this principle. This procedure may be logical between groups of squirrels that have the same likelihood of interacting to one another. Such may not be the case though for the interactions seen between adults and juveniles. In effect, it was shown that most interactions (85%) were initiated by adult squirrels. Accordingly, it is more meaningful to consider not only the average number of interactions happening between adults and juveniles, but also the average number of interactions initiated by an adult, and the average number of agonistic interactions to which a juvenile is submitted. Table 18 summarizes adult-young interactions in the usual manner, but also gives in parenthesis the seasonal averages of 1. agonistic acts initiated by an adult against a juvenile, and 2. agonistic acts to which juveniles were subjected to by adult squirrels. The three types of figures will be considered below.

In 1972, overall agonistic behavior between adults and juveniles averaged 8, 6 and 4 agonistic acts on plots 1, 2 and 3 respectively (Table 18). The plots did not differ significantly from one another in frequency of agonistic behavior (App. 15, no. 1). Treated squirrels were never seen to attack juveniles in 1972, while non-treated squirrels from plots 2 and 3 respectively averaged 6 and 4 agonistic encounters with juveniles (Table 18). Non-treated adults were significantly more aggressive to juveniles than treated squirrels on plots 2 while no difference could be shown between both groups on plot 3 (App. 15, no. 2). Treated squirrels were never seen to attack juveniles, nor to be attacked by them, and also were significantly less aggressive towards juveniles than non-treated adult squirrels(#2-1972). Still no significant difference in frequency of agonistic behavior could be shown between the control plot (#1) and the treated plots (#2, 3).

This lack of difference between plots is further illustrated when numbers of agonistic acts initiated by adults and suffered by juveniles are considered. In 1972, non-treated adult squirrels were aggressive towards juveniles on 26, 30, and 15 occasions (Table 18). No significant difference could be shown between any of these averages (Mann-Whitney tests), although it appears that non-treated squirrels from plot 3, the least dense plot, may have been less aggressive than non-treated squirrels from denser plots (Table 19). On average, each juvenile was submitted to 13, 12 and 16 agonistic encounters on plots 1, 2 and 3 respectively (Table 18). Again, no significant difference could be shown between treated and non-treated plots.

In 1972, when active squirrel densities of 18.2, 15.1 and 8.6 adults, and 23.0, 24.9 and 9.0 juveniles are combined on plots 1, 2 and 3 respectively (Table 19), it appears that the total densities were not significantly different between plots 1 and 2 (Mann-Whitney, N.S.), while being greater on plots 1 (Mann-Whitney, S. 99) and 2 (Mann-Whitney, S.99) than on plot 3. Moreover, the relationships between plots were the same when adult and juveniles densities were compared separately. In spite of the plots' differences in active squirrel densities, no difference could be shown between the levels of adult-young agonistic interactions observed on the three plots in 1972.

iv. Frequency 1973

In 1973, adult-young agonistic interactions averaged 7, 2 and 1 agonistic acts (per 45-minute per 100 squirrels) on plots 1, 2 and 3 respectively (Table 18). No difference was observed between the control plot and plots 2 and 3 (App. 15, no. 1). When groups of squirrels were compared within plot 2-1973, no difference was found between treated and non-treated squirrels (App. 15, no. 2). Groups of non-treated squirrels did not differ either when comparisons were made between plots 1, 2 and 3 (App. 15, no. 3), as they interacted with juveniles in averages of 7, 3 and 1 agonistic interactions (Table 18).

When the levels of adult agonistic behavior towards juveniles were calculated in function of the numbers of adults only and were compared, it was seen that adults from the control plot (34 acts) interacted agonistically with juveniles more often than the adults from plot 3 (1.4 acts), while they did not differ from adults on plot 2 (24 acts) (Mann-Whitney, N.S.) (Table 18). When the average number of agonistic interactions to which a juvenile was submitted were compared (per juvenile only), no difference could be shown among plots (Mann-Whitney tests). It is most likely that such a lack of difference was due to the small sample size involved, as averages greatly differed .

In 1973, plots 1 and 2 had equivalent adult densities, i.e. 18.2 and 20.9 active adults per 45-minute period (Table 19; Mann-Whitney, N.S.). Adult density of 9.4 on plot 3 (Table 19) was significantly less than observed on plots 1 (Mann-Whitney, S.99) and 2 (Mann-Whitney, S.99). However, the total numbers of young born or immigrating onto plots 2 and 3 were lower in 1973 (Table 7). Juvenile densities on plot 2 (Mann-Whitney, S.97.5) and plot 3 (Mann-Whitney, S.97.5) were less than on plot 1; in effect, only 6.0 and 4.6 juveniles were active on plots 2 and 3 compared with 34.9 on plot 1 (Table 19). As a consequence, combined adult and juvenile densities were significantly lower on plots 2 (Mann-Whitney, S.99.5) and 3 (Mann-Whitney, S.97.5) than on plot 1.

Given the total densities observed on the 3 plots, and the mestranol treatment given in one of them, I expected that in 1973 levels of agonistic interactions should be lower on plots 2 and 3 than on plot 1. Such was not the case and the only indication of an effect of the mestranol treament was the fact that again no treated squirrels was ever seen to react aggressively to a juvenile (Table 18). Density may have had some influence. Adults were more aggressive towards juveniles on the control plot than on plot 3 which was not treated either in 1973. Both adult and juvenile densities were high on plot 1. Adult population was normal on plot 3, i.e. low as compared to plot 1, and juvenile population was very low. On the other hand, adult aggression towards juvenile was the same on plots 1 and 2, plots which had similar adult densities in 1973. It thus appears that levels of adult-young agonistic behavior may be related to density.

v. Frequency 1972 versus 1973

No statistical difference could be shown between the levels of adult-young agonistic behavior on any of the plots between 1972 and 1973 (App. 15, no. 1). No changes could be shown for either treated (App. 15, no. 4) or non-treated (App. 15, no. 3) groups of squirrels between the 1972 and 1973 seasons (Table 18).

When the numbers of agonistic encounters directed towards juveniles by adults were calculed per adult present, and were compared between 1972 and 1973, no differences could be shown on plot 1 (26 versus 34), plot 2 (24 versus 3) or plot 3 (12 versus 1.4) (Table 18; Mann-Whitney tests). However, when the numbers of agonistic interactions experienced per juvenile were compared between 1972 and 1973, a significant difference was shown on plot 2. Juveniles on plot 2-1972 were the recipient of more aggressive acts than juveniles from the same population in 1973 (Table 18; Mann-Whithney, S.95). Such a difference was not observed on plots 1 and 3.

In 1973, the total density of active squirrels did not change on the control plot when compared to that of plot 1-1972 (Mann-Whitney, N.S.; Table 19); the fact that levels of adult-young agonistic interactions were the same in 1973 as in 1972 was as expected. However, total densities of active squirrels were significantly lower on plots 2-1973 (Mann-Whitney, S.97.5) and 3-1973 (Mann-Whitney, S.97.5) than they were on the same plots in 1972 (Table 19). Data from Table 18 shows a concurrent decrease of aggression between adults and juveniles on these plots in 1973; 6 and 4 adult-young agonistic acts were observed on plot 2-1972 and 3-1972 while only 2 and 1 were recorded on these same plots in 1973 (Table 18). The low level of interaction observed did not allow any statistical difference to be shown between the levels of aggression observed on plots 2 and 3 in 1972 and 1973 (App. 15, no. 1), with the exception of the number of adult agonistic acts to which the juveniles were submitted to on plot 2-1973. A reduction in the number of juveniles born and active on this plot, as well as a reduction of the number of adult residents, were followed by a decrease in the level of adult aggression towards juveniles. However, the fact that mestranol treatment was more intense in plot 2-1973 than in plot 2-1972 should also be taken in consideration. This factor would most likely also contribute to decrease the levels of adult-young aggression.

b. Plots (1), 4, 5 and 6

Seventeen, 15 and 25 juveniles were trapped on plots 4, 5 and 6 in early June 1973, accounting for densities of 42.5 , 37.5 and 62.5 juveniles per hectare (Table 22). At the same time, 54 juveniles were present on plot 1 (Fig. 4), at a density of 83.1 per hectare (Table 22). When juvenile and adult numbers are combined, 104.6, 55.0, 47.5 and 82.5 squirrels were found to be present on plots 1, 4, 5 and 6 during June 1973 (Table 22). The density on the control plot was thus roughly twice that on plots 4 and 5, and 1.3 times that of plot 6.

During June 1 - August 28, 1973, densities of 35.3, 22.7, 23.5 and 28.2 active juveniles were observed on plots 1, 4, 5 and 6 resulting in combined adult-young active densities of 51.5, 28.5, 30.4 and 39.0 squirrels per hectare (per 45-minute observation period) (Table 23). When combined adult-young densities are compared, it appears that plot 1 had a greater active squirrel density than plots 4 and 5, but did not differ from plot 6; plot 6 had a greater active squirrel density than plot 4, but did not significantly differ from plot 5 (App. 14, no. 2).

Adult-young agonistic encounters averaged 9, 10, 39 and 36 agonistic acts (per 45-minute per 100 squirrels) on plots 1, 4, 5 and 6 during the June 1 - August 28 period (Table 24). When the levels of agonistic behavior were compared on plots 4, 5 and 6, they were shown to be directly related to the densities of squirrels on these plots. Plot 5 did not differ significantly from plots 4 and 6 in density (App. 14, no. 2), nor in levels of agonistic behavior (App. 14, no. 5). Plot 6 had a higher density than plot 4 (App. 14, no. 2) and was characterized by a higher level of adult-young agonistic behavior (App. 14, no. 5). The levels of aggression on plot 1 were consistently lower than expected if the same relationship between density and behavior as observed on plots 4, 5 and 6 was to hold. Densities of active squirrels were the same on plots 1 and 6 (App. 14, no. 2), but levels of agonistic behavior were higher on plot 6 (App. 14, no. 5). Densities of active squirrels were higher on plot 1 than on plots 4 and 5 (App. 14, no. 2), but levels of agonistic behavior were basically the same on all plots (App. 14, no. 5). Overall, plots 4, 5 and 6 had greater levels of agonistic behavior than the control plot given their observed density relationships.

I suggest that more agonistic interactions were taking place on plots 4, 5 and 6 because of a greater external disturbance of animals on these plots. Plots 4, 5 and 6 were trapped in June 1973 when both adults and juveniles were present. Squirrels from these plots were not as used to the presence of the observer as squirrels on plot 1. Adult squirrels from plot 1 had already been trapped many times, some of them both in 1972 and 1973; they had been observed since March and had thus seen the observer on a daily basis for a period of at least 3 months. Juveniles from plot 1 were trapped as soon as they emerged from the maternal burrow; they showed little fear and were easily handled, marked and caressed by the observer. This was not the case for squirrels on plots 4, 5 and 6; being trapped was a new experience and they were not accustomed to the observer's presence. I suspect that such greater disturbance could have resulted in a greater nervousness and possibly in the increased levels of agonistic interactions observed on these plots. Such was the case for adult-young interactions, and it could have been the case for adults (Table 24), although statistical tests there were not significant. Adult-adult agonistic interactions averaged 40 agonistic acts on plots 4, 5 and 6 when only 4 were observed on plot 1 (Table 24). Adult-young interactions averaged 28 agonistic acts on plots 4, 5 and 6 while only 9 were observed on plot 1 (Table 24). If the hypothesis is correct, the same phenomena should be observed for the young-young agonistic interactions on these plots.

c. Summary: Adult-young interactions

1. One-hundred seventy five agonistic interactions were recorded on plots 1, 2 and 3 between adults and young in 1972 and 1973, representing only 15% of the total number of agonistic acts observed on these plots.
2. The most common type of encounter was the chase (60%), and all other forms of agonistic encounter, i.e. fight, threats, etc. were observed in roughly the same proportions as amongst adults. The bite was peculiar to adult-young interactions and represented as much as 15% of all adult-young interactions.
3. Juveniles were dominant in only 15% of the adult-young agonistic interactions and most of these were observed between resident juveniles and transient adult squirrels. Moreover, the interactions where juveniles were dominant occurred only in late summer (June-July) when adults were less aggressive and were preparing for hibernation.
4. Each year, agonistic behavior between adults and juveniles started soon after juveniles first emerged from the burrows; such behavior was at a low level for the first 20 days after emergence and subsequently reached a peak. Agonistic encounters then became less frequent and ceased about 14 days before the adults went into hibernation.
5. Overall, no difference in the intensity of adult-young agonistic behavior could be detected between plots 1, 2 and 3 in 1972 or 1973 as the total number of such interactions was low. No difference existed either within any of the plots between 1972 and 1973.
6. However, adult-young aggression may have been influenced by the mestranol treatment. Treated squirrels were never seen to behave agonistically to juveniles, which was not the case for non-treated squirrels.
7. The influence of population density on adult-young agonistic behavior was indicated by the following observations:
   a. at high density, non-treated squirrels were more aggressive to juveniles than treated squirrels (plot 2-1972). At low density, no differences could be found between the two groups (plot 3-1972).
   b. non-treated squirrels directed more aggressive acts towards juveniles on high density plots than on low density plots (plot 1 versus plot 3, 1973)

   c. a decrease in the number of juveniles brought a decrease in the number of agonistic adult encounters to which these juveniles were submitted (plot 2-1972 versus plot 2-1973)
   d. the levels of adult-young agonistic interactions were apparently related to the combined densities of adults and juveniles on plots 4, 5 and 6. When combined adult and juvenile densities on plots were similar, the levels of agonistic interactions were also similar; if the density of active squirrels was higher on one plot than on another, the level of adult-young agonistic interactions showed the same relationship.

8. Levels of adult-young agonistic behavior may also have been influenced by the observer's presence. The levels of adult-young agonistic interactions on plots 4, 5 and 6 were consistently higher or equal to those observed on plot 1 although the density of active squirrels was either equal to or lower than that observed on plot 1. Squirrels on plots 4, 5 and 6 had been quite suddenly exposed to trapping and to the presence of the observer when compared to squirrels on plot 1.

3. Young-young interactions

a. Plots 1, 2 and 3

i. Types of interactions

A total of 458 agonistic interactions were observed among juveniles on plots 1, 2 and 3 during 1972 and 1973 (App. 4), representing 38% of the 1197 agonistic acts observed on these plots.

The chase (59%) was the most common type of agonistic interaction observed among juveniles and was often combined with fight (8%) or fight sec. (2%). The latter also occurred on their own, fights - 17%, fight sec. - 8%. Threats (5%) and face-off/avoidance (0.4%) were less common. No difference was observed as to the types of interactions occurring between littermates or between non-related juveniles (Chi-square, N.S.) (App. 9B). Similarly, juveniles were involved in the same types of interactions as the adults, with the exception of the bite, and interactions were observed in basically similar proportions to those seen among adults, and between adults and juveniles (Chi-square tests).

ii. Seasonal timing

On all plots where juvenile agonistic behavior was observed each year, young-young agonistic interactions never started within the 10-day period during which the first juveniles emerged, but were always recorded before the end of the next 10-day period (Fig. 7).

On plots where juvenile-juvenile interactions were seen, such agonistic acts were recorded without interuption from onset until the end of the observations each year, i.e. August 12 in 1972 and August 28 in 1973 (Fig. 7). Generally, the last 10-day period of observation was characterized by a drop in the level of agonistic interactions among young (Fig. 7), but as fluctuations had already occurred I assume that some young-young agonistic behavior continued after the end of the observations.

iii. Frequency 1972

In 1972, agonistic behavior among juveniles averaged 19, 17 and 12 agonistic acts (per 45-minute per 100 squirrels) on plots 1, 2 and 3 respectively (Table 25). Although the data indicated that young-young agonistic behavior may have decreased with the intensity of the mestranol treament given, no significant difference could be shown between any of the plots (App. 15, no. 5).

Table 25. Average numbers of agonistic interactions observed between juvenile squirrels (per 45-minute observation period, per 100 squirrels).

10-day period	PLOT 1			PLOT 2			PLOT 3		
	Litt	YY	All young	Litt	YY	All young	Litt	YY	All young
1972									
1	-	-	-	-	-	-	-	-	-
2	0	-	0	-	-	-	-	-	-
3	0	0	0	0	-	0	0	-	0
4	1	10	11	0	-	0	1	-	0
5	9	20	29	0	9	9	4	-	4
6	12	22	34	0	16	16	5	2	5
7	9	34	43	6	24	29	0	10	10
9	3	9	12	4	20	23	19	29	35
10	1	28	29	7	26	32	13	24	28
11	2	15	14	12	24	31	0	12	12
10-day average	4	17	19	4	20	17	5	15	12
1973									
0	-	-	-	-	-	-	-	-	-
1	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-
3	0	-	0	0	-	0	-	-	-
4	1	-	1	0	0	0	0	-	0
5	4	-	4	0	0	0	0	0	0
6	50	-	50	-	0	0	0	0	0
7	39	-	39			NO	0	0	0
8	28	-	28			NO			NO
9	13	-	13			NO			NO
11	14	0	13			NO	0	0	0
12	28	0	23	0	0	0	0	0	0
13	0	0	0	0	0	0	-	-	-
10-day average	18	0	17	0	0	0	0	0	0

When juvenile agonistic interactions were divided in two groups, i.e. those occurring among littermates, and those occurring among juveniles that are not related, it appears that more agonistic interactions occurred among non-related juveniles than among littermates (App. 15, no. 6). Littermates averaged only 4, 4 and 5 agonistic acts among themselves on plots 1, 2 and 3, while interactions among non-related juveniles accounted for 17, 20 and 15 agonistic interactions throughout the summer (Table 25). The intensity of agonistic behavior was not significantly different between plots for littermates (App. 15, no. 7), even though plots 1 (Mann-Whitney, S.99) and 2 (Mann-Whitney, S.99) had greater densities of active juveniles than plot 3 (Table 26). Similarly, no difference was observed between plots when levels of agonistic behavior were compared for non-related juveniles in these plots (App. 15, no. 8), although plot 3 had an immigrant juvenile population of twice the numbers seen on plots 1 and 2 (Table 7). However, it is possible that some of these immigrating juveniles were littermates, since their parentage was not known.

In 1972, no difference could be seen between plots 1, 2 and 3 on the effect of treatment and density on juvenile agonistic behavior. Juveniles on treated plots, and on low density plots were subjected to as much aggression from other juveniles as were juveniles on a high density, non-treated plot. The only difference observed was that juveniles interacted less aggressively towards their littermates than to unrelated individuals, and this occurred both on treated and non-treated plots.

iv. Frequency 1973

In 1973, an average of 17 agonistic interactions was observed among juveniles on the control plot, while no such interactions were ever observed among young from plots 2 and 3 (Table 25). Non-related juvenile interactions were not observed on any plots in 1973, although juveniles from many resident litters as well as immigrating juveniles were present on all plots (Table 26).

This lack of aggression in plots 2 and 3 as compared to plot 1 was probably due to the small numbers of juveniles on the former plots. In effect, more juveniles, i.e. 34.9 per observation period, were seen on plots 1 than on plot 2 - (6.0 juveniles; Mann-Whitney, S.99) and plot 3 (4.6 juveniles; Mann-Whitney, S.99.9) (Table 26). Juvenile populations on plots

Table 26. Average densities of active juvenile squirrels present on plots 1, 2 and 3 during an average 45-minute observation period in 1972 and 1973.

10-day period	PLOT 1			PLOT 2			PLOT 3		
	Yborn	Yout	All young	Yborn	Yout	All young	Yborn	Yout	All young
1972									
1	-	-	-	-	-	-	-	-	-
2	1.2	-	1.2	-	-	-	-	-	-
3	22.0	0.3	22.3	4.3	-	4.3	1.2	-	1.2
4	28.0	0.9	28.9	14.2	-	14.2	2.2	-	2.2
5	24.3	1.2	25.5	26.7	3.2	29.9	5.4	0.5	5.9
6	22.5	1.2	23.7	27.0	4.0	31.0	4.7	5.6	10.2
7	27.2	2.5	29.7	30.4	4.3	34.8	3.5	9.3	12.7
9	25.1	1.5	26.6	20.3	2.9	23.2	4.3	8.3	12.6
10	16.9	8.0	24.9	25.8	5.8	31.6	4.7	11.4	16.0
11	15.4	8.9	24.3	23.8	4.3	28.1	3.0	7.7	10.6
10-day average	20.3	3.1	23.0	21.6	4.1	24.9	3.6	7.1	9.0
1973									
0	-	-	-	-	-	-	-	-	-
1	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-
3	22.6	-	22.6	0.3	-	0.3	-	-	-
4	44.1	-	44.1	8.7	2.3	11.0	1.6	-	1.6
5	36.2	-	36.2	4.3	1.4	5.8	2.5	1.2	3.7
6	53.8	-	53.8	0	5.8	5.8	2.5	1.2	3.7
7	45.1	-	45.1			NO	2.5	4.9	7.4
8	45.1	-	45.1			NO			NO
9	34.6	-	34.6			NO			NO
11	22.0	1.6	23.6			NO	2.5	4.9	7.4
12	18.0	4.6	22.6	1.4	7.2	8.7	2.5	1.2	3.7
13	20.0	1.5	21.6	1.4	2.9	4.3	-	-	-
10-day average	34.1	2.6	34.9	2.7	3.9	6.0	2.3	2.7	4.6

2 and 3 did not differ (Mann-Whitney, N.S.). These low populations of juveniles in these plots are thought to result primarily from the overall failure of females to produce litters in these plots in 1973 (Table 7).

v. Frequency 1972 versus 1973

Levels of agonistic interactions among all juveniles did not differ significantly on plot 1 between the 1972 and 1973 seasons (App. 15, no. 5), in spite of a significant increase of the number of active juveniles on this plot (Table 26; Mann-Whitney, S.95). However there was more aggression among plot littermates in 1973 than in 1972 (App. 15, no. 7). The fact that no overall difference for all juveniles could be found was the result of a concurrent increase of littermate aggression and a decrease of non-related juvenile interaction (App. 15, no. 8). Only a few immigrants attempted to move onto plot 1 at the end of the summer 1973, when number of born juveniles was already much reduced (Fig. 5) so that there was little confrontation. Secondly, it seems that littermates were fully occupied interacting aggressively towards each other, and spent little time interacting agonistically with their juvenile neighbours. More juvenile residents were left in late summer 1973 - 21 juveniles active in August 1973 compared with 15 in August 1972 (Fig. 4). Thus in spite of increased aggression among littermates, more juveniles were left as residents in 1973 suggesting that 1973 was a year favourable to juveniles on the control plot.

There was a very significant decrease in the levels of young-young agonistic interactions on plots 2 and 3-1973 as compared to the 1972 season (App. 15, no. 5). While as many as 17 and 12 agonistic acts were observed during 1972, none were observed in 1973 (Table 25). This decrease in juvenile agonistic behavior most likely reflects the drop in numbers of juveniles on these two plots in 1973 (Fig. 5). The reduction of young-young agonistic behavior on plots 2 and 3 in 1973 results mostly from the fact that no agonistic interactions took place among non-related juveniles that year, while significantly greater averages of 20 and 15 agonistic acts were recorded among these squirrels on plots 2 and 3-1972 (Table 25; App. 14, no. 8). The low number of interactions recorded did not permit significant differences to be shown in the levels of agonistic behavior observed among littermates on these plots in 1972 and 1973 (Table 25; App. 15, no. 7).

An increase in the density of juveniles born was related to an increase of littermate aggression and a decrease in non-related juvenile aggression on plot 1; as a result, no overall changes could be measured between 1972 and 1973 on this plot. Decreases in juvenile densities on plots 2 and 3 in 1973 were accompanied by concurrent decreases in the levels of agonistic behavior, especially among non-related juveniles, and possibly among littermates as well.

b. Plots (1), 4, 5 and 6

Densities of 83, 42, 37 and 62 juveniles were present on plots 1, 4, 5 and 6 in June 1973 (Table 22) and, on average, 35, 23, 23 and 28 of these were observed to be active during the behavioral observations made from June 1 - August 28 (Table 23). Significantly more juveniles were active on plot 1 than on plot 4 and 5 , while no statistical difference could be determined between the juvenile densities of plots 1 and 6 (App. 14, no. 3). No difference in density of active juveniles was seen between plots 4, 5 and 6 (App. 14, no. 3).

Averages of 21, 87, 79 and 47 agonistic encounters were observed among juveniles on plots 1, 4, 5 and 6 respectively (Table 24). Significantly more young-young agonistic interactions occurred on plots 4, 5 and 6 than on plot 1 (App. 14, no. 6), in spite of the fact that plot 1 had a higher juvenile density than plots 4 and 5 and had a similar density to plot 6 (App. 14, no. 3). No significant differences were observed in the density of active juveniles on plots 4, 5 and 6 (App. 14, no. 3), and similarly, no difference was observed in the levels of agonistic interactions observed (App. 14, no. 6).

These results therefore support the hypothesis put forward in the previous section, i.e. greater external disturbance on plots 4, 5 and 6 resulted in higher levels of agonistic behavior.

c. Summary: Young-young agonistic behavior

1. Young-young agonistic interactions represent 38% of all agonistic acts recorded on plots 1, 2 and 3 during 1972 and 1973.
2. The chase (59%) was the most common type of agonistic encounter, and was frequently observed in conbination with other forms of aggression such as the fight and fight sec.
3. Aggression among juveniles started betweeen 10 and 20 days after a juvenile emergence was observed on each plot. Levels of agonistic interactions fluctuated but maintained themselves throughout the summer and juveniles were still agonistic to one another when field observations were stopped in late August each year.
4. In 1972, no statistical differences could be found in the levels of juvenile agonistic interactions when the treated plots (#2,3) were compared to the non-treated plot (#1), even though there were differences in the densities of juveniles active on the plots. More agonistic encounters were observed between non-related juveniles than between littermates on all plots.
5. In 1973, density of juveniles was drastically reduced on plots 2 and 3 while it increased on plot 1. As a result, agonistic interactions were less numerous on plots 2 and 3 than they were on plot 1.
6. A decrease in juvenile density on plot 2 and 3 in 1973 as compared to 1972 was related to a decrease of agonistic behavior among juveniles on these plots.
7. Levels of young-young agonistic interactions were similar on plots 4, 5 and 6 and these plots had similar densities of active juveniles. Plots 4, 5 and 6 had higher levels of young-young agonistic interactions than noted on the control plot (#1). This occurred despite the fact that these plots had either equal or lower densities of active juvenile squirrels. This high level of aggression on plots 4, 5 and 6 was attributed to the disturbance created by the presence of the observer.
8. The number of juveniles born and active on the control plot was greater in 1973 than in 1972. This resulted in an increased number of agonistic interactions observed among littermates. Fewer juveniles immigrated onto the plot, and agonistic encounters among non-related juveniles decreased. Overall, as a result of these concurrent increases and

decreases of agonistic behavior among different classes of juveniles, no difference was observed in the levels of agonistic behavior of the total juvenile population between 1972 and 1973.

9. It seems that an increase in juvenile numbers resulted in an increase in aggression, at least for littermates, and that a decrease in juvenile numbers meant a decrease in aggression among non-related juveniles, and possibly among littermates as well.
10. The mestranol treatment did not have an effect on young-young agonistic behavior as such. However, by modifying the density of juveniles, it indirectly changed the frequency of agonistic interactions among juveniles.

DISCUSSION

A. Introduction

Populations fluctuate within a year from one area and another, and also from year to year as the balance between their recruitment and their losses changes. Breeding and immigration increase numbers, while mortality factors and emigration decrease them. For a given population to maintain itself, recruitment has to equal or be greater than losses. However the density of a population has to remain below a certain level to keep it from over-exploiting its resources (Wynne-Edwards, 1962).

One school of thought assumes that unlimited increases of populations are prevented entirely by external factors such as weather, food supply, predation, etc. (Nicholson, 1933; Andrewartha and Birch, 1954; Thompson, 1956). Other researchers think that population containment can be achieved through self-regulation (Chitty, 1960). Self-regulation would allow populations to fluctuate with prevailing environmental conditions, but would limit any increase that threatens to destroy a population′s resources.

The first rule of population self-regulation is that no population stops increasing unless either the birth rate or the death rate is density dependent (Krebs, 1978). It is also postulated by Wynne-Edwards (1962) that populations establish self-regulation by competing, not for the food resource itself, but rather for a substitute that allows optimal allocation of the resources. Such may be the function of territorial behavior that spaces the individuals in the suitable environment. This assumes that the size of the territory is directly related to the productivity of the environment and will effectively adjust a population to its food supply (Gibb, 1962).

Self-regulatory responses to changes in density or environmental conditions can be physiological (Christian and Davis, 1964), genetical or behavioral (Chitty, 1960 and 1967). If behavior is the proximal factor limiting a population, it is generally assumed to operate via a socially-induced mortality, or via a socially-induced depression of recruitment (Watson and Moss, 1970). Birth rates are often assumed to be constant and independent of population density so that all attention is focused on mortality rates (Varley et al., 1973, as cited in Krebs, 1978).

However, Davis (1951) in populations of Norway rats, and Kalela (1957) and Hoffmann (1958) in populations of voles, have shown an inverse relationship between natality (as measured by ovulation rate or litter size) and population density.

If animals do regulate their numbers, it has not been determined yet at what level(s) they do so (Watson, 1971). Populations could be kept high so as to be reduced quite often by changes in food supply. They could choose an optimal level which would allow a maximum number of individuals but without over-utilization of the resources. Or populations could be kept so low that food would have no effect on them. Territorial behavior should be affected by the levels at which populations are regulated (Brown, 1964). At low density, territory size should not be limited by competition. At mid-density, a few individuals should be excluded, but could use poorer habitat and still breed, offering a buffer population for unexpected fluctuations. At high density, a surplus of individuals would be unable to breed and a floating population would be formed, subject to higher mortality factors (Christian and Davis, 1964).

Social behavior, and especially agonistic behavior, probably plays an important role in population control by influencing birth, death and movements. Lloyd and Christian (1967) have summarized much of the work on confined mouse populations and concluded that aggression affects birth rate mostly through physiological mechanisms. Aggressive behavior varies with the stage of breeding cycles in mammal species (Beach, 1947; Sadleir, 1965). The reproductive performance of female woodchucks (Marmota monax) is affected by the sex ratio of a given population as mediated through the intensity of social stimuli originating from the presence of adult males in the population (Snyder, 1962). The effect of agonistic behavior on death rate and movement seems less clear. Emigration of yearling marmots (Marmota flaviventris) is related to the agonistic behavior of the adults (Armitage, 1962), while Bronson (1964) had good evidence that woodchucks disperse during a period of declining aggressiveness. A relationship was established between the aggressive behavior of adult males and the survival of juveniles in deer mice (Healy, 1967). In the Richardson's ground squirrel, Yeaton (1972) saw no relationship between juvenile dispersal and agonistic behavior, while Dorrance (1974) considers that juvenile dispersal is density-dependent. Burns (1968) established that agonistic behavior acted as a controlling factor for the Uinta ground squirrel in the spring when breeding territories were established, and in late summer, when dispersal of well over half the juveniles was related to aggression. Balph (1970) and Slade (1971) considered density-dependent dispersal of the young to be fundamental to the population regulation of this same species. Similarly, territoriality among adults determines the breeding population in the Arctic ground squirrel, while young are driven out of their natal burrows by the increasing belligerence of their mother (Carl, 1971). In the round-tailed ground squirrel, agonistic behavior can affect the dispersal of juvenile and adult squirrels. However social behavior cannot regulate population densities when the food supply is improved and predation reduced (Dunford, 1977a). Overall, there is good evidence that social behavior plays an important role in the control of animal populations, and especially so for territorial species.

A unique situation was created during the present study. Normally, animal population studies deal with numerical fluctuations between years or between areas and attempt to establish relationships between different factors. Alternatively, populations are modified, usually by the removal of a segment of the population. In both cases, changes in numbers are related to changes in the environment, be they weather, vegetation, or the social structure within a population in a case of removal. But in the present study, we have the usual combination of comparisons between years or between areas, but we also have the case of the treated populations. The treatment initially did not modify the numbers of individuals present nor the sex ratio or the age structure of the population. No squirrel was removed; within a given year and a given plot, the food supply did not change. What had changed was the physiological conditions of some of the adult squirrels; their ability to breed had been suppressed. All other factors being equal, it was expected that any differences in numerical or behavioral fluctuations between a treated and a non-treated plot should be related to treatment. Such differences should mostly show up in the adult population, and possibly in the relationship between the adult and juvenile segments of the populations.

The mestranol treatment effectively sterilized all but one of the females treated. Treated females gained weight faster than breeding females and returned into hibernation sooner than the latter, when initial body weight was the same in April. Treated females were also characterized by a different frequency of social behavior when compared to non-treated females. Proportionally more cohesive interactions occurred between non-related adults and juveniles on the treated plots than on the non-treated plots. Overall, treated squirrels seemed to be more tolerant. This was illustrated clearly by the fact that, contrary to non-treated adults, treated squirrels were never observed to behave aggresssively towards juveniles. Secondly, on a high density plot, treated squirrels behaved less aggressively than non-treated squirrels towards other adults, and readily shared their core area with other adults. This effect of the treatment on the physiology and the social behavior of the treated squirrels influenced the populations as a whole.

I propose to analyze the changes brought about in the adult and juvenile populations by the treatments given, and to establish other relationships pertinent to the theoretical considerations previously cited. Food supply, weather, predation, population density itself and social behavior are factors that will be considered.

B. Annual cycle

1. Emergence from hibernation

The spring emergence of squirrels was not studied in detail and the impact of behavior or treatment could not be ascertained. However, other factors influencing emergence became evident.

Squirrel emergence occurred in March in 1972 and 1973, while it was much delayed in 1974. It was only on April 25, 1974 that it was assumed that all squirrels had emerged and were trapped; in 1972 and 1973, all squirrels were trapped by April 1.

Spring was much delayed in 1974. Snow was left on the ground until April 23, while it was gone by the second or third week of March in 1972 and 1973. This probably resulted because more snow fell during the 1973-1974 winter than during the two previous winters and that generally, temperature was colder during the spring of that year.

Emergence of individuals is related to snowmelt in the golden-mantled ground squirrel; food becomes available only when the snow is gone (Bronson, 1977). In the Uinta ground squirrel, emergence and subsequent events are determined, within limits, by spring temperature (Knopf and Balph, 1970). In the Richardson's ground squirrel, emergence, and hence breeding, are affected by increasing daily temperature in late March and early April (Michener, 1973a).

The conscensus is that spring weather conditions are a major determinant in the timing of emergence from hibernation which in turn affects the timing of breeding. The evidence gathered during the present study supports these observations.

2. Breeding and parturition

Breeding normally occurs from two days (Michener, 1977) to two weeks after emergence (Yeaton, 1972) for adult females. As such, breeding should be mostly determined by the factors affecting the emergence of squirrels from hibernation. However, other factors are involved as well.

Breeding consistently occurred earlier on plot 1 than on plots 2 and 3, as shown by the earlier emergence of juveniles. Heavier females breed earlier than light females (Dorrance, 1974). This was also seen in this study as females from plot 1 were consistently heavier than females from plots 2 and 3. Differences in body weight at the same date on different plots could have been due either to different emergence times, or to a different availability of food supply. However, as emergence was primarily determined by the spring temperature regime, which must have been relatively the same as the plots were geographically in a small area, the difference in body weight seen can be attributed largely to the differences in food supply.

Breeding occurred earlier on plot 1 which was characterized by an additional source of food resulting from the winter feeding of cattle on the plot. A direct correlation exists between food supply and body weight in female ground squirrels (Dorrance, 1974). The food supply available in the spring, but especially the food supply from the previous year, would most likely influence females' body weight and hence breeding time. Further evidence gathered by Michener (1977a, 1978) and Wang (1973) indicates that adult females emerge at the same time in the spring, regardless of their breeding status and rate of fat accumulation during the previous summer; the hibernation season is shortened for squirrels that immerge late in the summer (Wang, 1973). Thus the time of breeding would have been determined primarily by time of emergence and was probably influenced by the weight of the breeding females, which in turn was most likely related to the food supply available for a given population.

3. Emergence of juveniles from the maternal burrow

Juveniles spend a month in the maternal burrow between birth and emergence (Michener, 1974). The average date of juvenile emergence is likely related to the date of breeding and parturition, and hence to the prevailing spring weather. The average date of breeding was also related to the food supply available as translated by females' body weight. Moreover, it is possible that the average stay of juveniles in the maternal burrow between birth and emergence could also be influenced by food supply. Juveniles being nursed by heavier females could grow faster than juveniles having lighter weight mothers and thus could emerge earlier. Post-natal losses have been related to the quality of the food supply and to the resulting capacity of females to lactate and nurse their young in the Richardson's ground squirrel (Michener, 1972; Dorrance, 1974). The fact that each year, juveniles emerged earlier on plot 1 than on plots 2 and 3, a plot characterized by the presence of a better food supply, supports such a hypothesis. However, the data necessary to establish such a relationship was not collected during this study.

Time of juvenile emergence could not be shown to be related to population density or treatment. Each year, emergence of juveniles was later on plot 2 than on plot 1 although these two plots had similar adult densities. Juveniles from plots 2 and 3 emerged at the same time in 1973, although plot 2 was treated, and plot 3 was not.

Emergence of juveniles could not be shown to be related to social behavior either. Only the adult-adult behavior would affect the juveniles' mother and possibly the juveniles themselves. The level of adult-adult agonistic interactions (10-day periods 1-4) was higher on plot 1 in 1972 than in 1973; yet average date of juvenile emergence was the same on this plot each year.

Juvenile emergence was primarily determined by the average dates of adult emergence in the spring, and hence breeding, and by the average body weight of their mother as determined by weather and food supply. Factors such as population density, mestranol treatment and adult-adult behavior did not seem to have any bearing.

4. Onset of hibernation

In 1972 and 1973, treated females and adult males hibernated earlier than non-treated females, and juveniles were the last to hibernate. Thus breeding status, sex and age were all factors to be considered.

The dissimilarities observed between groups of squirrels seemed to be mediated through weight differences. Adult males and non-breeding females accumulated weight faster than breeding females. Michener (1978) showed that non-parous females steadily gain weight between emergence and immergence into hibernation, while parous females undergo cycles of weight losses and gains resulting in delayed attainment of pre-hibernation peak weight and delayed entry into hibernation. Juveniles were the last to hibernate. Each year, adult Richardson's ground squirrels gain at least 200 g, while young gain at least 300 g under natural conditions (Hansen and Reed, 1969). Differences in weight or in weight increases were also linked to differences in the food supply available. Breeding females from plot 1, which benefited from a "better" food supply, were heavier than breeding females on plots 2 and 3. They consistently went into hibernation earlier than the latter. Moreover, average onset of hibernation occurred earlier in 1973 than in 1972; in 1973, vegetation was lusher than in 1972. A significant correlation has been shown to exist between biomass of vegetation and adult females' weights and weight gains in populations of Richardson's ground squirrels in central Alberta (Dorrance, 1974). Thus the changes in the food supply likely also affected the onset of hibernation of ground squirrels in my area.

Overall, differences in onset of hibernation were linked to the metabolic demands of a given group of squirrels and to their ability to fulfil them. Breeding female rodents have greater energy demands than non-breeding females and adult males (Sadleir et al., 1973), and thus female ground squirrels apparently required more time above ground to accumulate the body fat necessary to a successful hibernation. Juveniles, which first had to grow, needed the longest activity period to put on weight for hibernation. It was easier to accumulate such weight on plots with a better food supply, or during a year characterized by greater rainfall and hence lusher vegetation.

These metabolic demands, as well as being linked to sex, age, breeding status and food supply, may also be influenced by the populations' densities and their levels of social behavior. Adult males and females from plots 2 and 3 had similar body weights, but resident density was greater on plot 2 than on plot 3 each year. Concurrently in 1972, adult males and breeding females from plot 2 returned into hibernation later than their counterparts on plot 3. However, they did not do this in 1973. This difference between years may have been mediated through changes in social behavior and/or food supply. In 1972, breeding squirrels on plot 2 were more aggressive than on plot 3; there was no difference between the two groups in 1973. This could result from the better food supply observed in 1973. An adequate food supply being more accessible in 1973 could have reduced competition and made social aggression less necessary for squirrels. The fact that density and behavior can influence the energy expended by the different squirrels, and hence the onset of hibernation is plausible considering the evidence gathered by Ruff (1971) in populations of Uinta ground squirrels. A radio-telemetry field study of these squirrels showed that animals in crowded areas or with a history of much aggression responded more, in terms of the magnitude of their heart rate, to social interactions or stress than squirrels from less crowded areas. Such results could account for the observation made on plot 2, where adults of same weight and breeding status as those on plot 3, hibernated later. The higher density, and thus "social stress" on plot 2, could account for greater energy expenditure and for delayed hibernation.

The average dates of hibernation onset observed on plots 1, 2 and 3 in 1972 and 1973 were thus the result of many factors. First, breeding status, age, sex, and food supply influenced the body weight of individuals and their rate of fat accumulation, and therefore influenced the onset of hibernation. Secondly, density of population and levels of agonistic interactions could also influence the rate of weight gains in a situation of poor food supply, and thus also affect the onset of hibernation.

C. Population dynamics

1. Annual survival

Of the adults first trapped on plot 2 in 1972 and surviving to April 1973, proportionally more treated squirrels survived than non-treated ones. This relationship could not be established the second year since very few squirrels on plot 2 were left unaffected by mestranol. Adult survival remained the same during the 1972-1973 and 1973-1974 winters on plots 1 and 2; each year these two plots had the same treatment regime, i.e. plot 1 as a control and plot 2 roughly 50% treated. By contrast, plot 3 was treated in 1972 and was not in 1973. Adult survival dropped significantly on plot 3 during the 1973-1974 winter, indicating that the 1972 mestranol treatment may have allowed for a better than normal survival on that plot during the 1972-1973 winter. The possibility of treated squirrels' survival being better is confirmed by the fact that treated squirrels accumulated weight faster than non-treated squirrels and hibernated earlier than the latter. A significant correlation exists between overwinter survival and body weight of squirrels in June; heavier squirrels have a better survival than lighter squirrels (D.R. Michener, 1972). Thus, non-breeding individuals had a better survival than those which bred, possibly a result of their abiltiy to accumulate weight faster and hibernate sooner. Such a relationship was partly shown by Michener (1978) in Richardson's ground squirrel. Older breeding females needed a longer time than younger breeding females to attain pre-hibernation weight. As a result, they immerged later, and had a lesser overwinter survival than younger females.

Females survived better than males. This was also observed by other researchers (D.R. Michener, 1972; Dorrance, 1974). However, the treatment may have improved the survival of juvenile males on the treated plot so as to eliminate such a difference. On plot 2-1972, male juveniles survived as well as juvenile females to April 1973. Such was not the case on the control plot, where as expected, juvenile females survived much better than juvenile males. Juvenile numbers were too small on plot 3-1972 and plot 2-1973 to make this comparison again. A "good" burrow is essential to successful hibernation and survival for the Richardson's ground squirrel. Hibernation burrows are first taken by adult females and males, then by the juvenile females and lastly by the juvenile males; the latter group of squirrels goes into hibernation last and is usually left with sub-optimal burrows for hibernation (Michener and Michener, 1977). This could partly account for juvenile males' survival normally being the lowest. On treated plots, this disadvantage of juvenile males seems to have been reduced. Their survival was improved, and in April 1973, significantly more males were present on the two previously treated plots than on the control plot. Wehrell (1973) showed that dominant females occupy a central position within a colony of Richardson's ground squirrels. Such a home area location would no doubt increase chances of survival, especially when terrestrial predation is involved. Possibly in the treated plots, juvenile males were allowed to maintain themselves in more of a central location because of the reduced aggressiveness of treated adults towards juveniles then, hence their better chances of survival. Moreover, the fact that juvenile density was reduced by treatment on plots 2 and 3, could also have reduced the competition for available burrows.

The harsher climatic conditions observed during the 1973-1974 winter were correlated with reduced squirrel survival. Bad spring weather (Nixon and McClain, 1965), and snow storms especially, can reduce squirrel survival and breeding success in populations of ground squirrels (Morton and Sherman, 1978) by preventing emerging squirrels from feeding. Emerging squirrels normally have some fat reserves left (Dorrance, 1974), but a snow cover remaining a month longer than usual would no doubt strain the squirrels' ability to survive until food is available. In such circumstances, starvation, death and cannibalism were observed in populations of Belding's (Morton and Sherman, 1978) and Richardson's ground squirrels (Dorrance, 1974).

These differences in survival due to weather changes affected some groups of squirrels more than others. Normally, adult females survive better than juvenile females (D.R. Michener, 1972; Dorrance, 1974). However, during the 1972-1973 winter, no difference could be shown between adult and juvenile female survival on any of the plots; such was not the case over the 1973-1974 winter. Juvenile female survival dropped on the control plot, while adult female survival remained the same. By contrast, adult and juvenile female survival was similar on the previously treated plots in 1973-1974. On the control plot, juvenile females were clearly disadvantaged in relation to adult females when climatic conditions became harsher. On the the treated plots, juvenile females had the same chances of survival as adult females in spite of worse climatic conditions. Thus treatment favoured a better survival of the juvenile females on the treated plots during a difficult winter. During 1972-1973, survival was the same for resident and non-resident adult squirrels. However, over the 1973-1974 winter, non-residents were disadvantaged; their survival dropped significantly when compared to that of the resident squirrels. This was so on plots 1 and 2, both high density plots, while it was not on plot 3. On the latter plot, density was low in 1972 and 1973, and although adult survival dropped between the 1972-1973 and 1973-1974 winters, it dropped for both resident and non-resident adults so that proportionally as many squirrels of each category survived to April 1974.

Overall, the improvement on the treated plots of annual survival for juvenile males and females, and for non-resident adults indicates that the treatment, either through changes in social behavior or in population density, reduced the competitive disadvantage of these categories of squirrels since their survival was relatively better during a hard winter than that of their counterparts on a non-treated plot.

The differential effect of climate on non-residents' survival according to population density was the first indication that density may affect squirrel survival. However, comparisons between plots were difficult considering the large impact of the mestranol treatment. Hence, a true measure of the effect of density could only be obtained on the control plot. On plot 1, resident adult density and born juvenile numbers were much higher in 1973 than in 1972. Juvenile survival dropped drastically during the second year as compared to the first year. This probably resulted from the harsher climatic conditions observed in 1973-1974 rather than from effect of increased density. However, it was observed that at the end of August 1973, no juvenile had yet gone into hibernation. By contrast, in 1972, many females had already gone into hibernation during the first half of August. Many more juveniles were born on plot 1 in 1973, more stayed on the plot and competed for the available food supply. Although vegetation was better in 1973 than in 1972, in terms of energy expenditure, it may have not compensated for the "social stress" created by greater juvenile densities. The later onset of juvenile hibernation and the higher frequency of agonistic interactions observed among littermates in 1973 support such a hypothesis. Thus, high density per se may reduce juvenile survival.

No difference in adult survival could be seen between plots 1, 2 or 3 each year. Concurrently, no differences in level of adult cohesive or agonistic behavior could be detected between the three plots. On the other hand, on plot 2-1972 where there were sizable portions of treated and non-treated squirrels, it was shown that treated squirrels were significantly less aggressive than non-treated squirrels. Interestingly, treated squirrels had a better survival than non-treated squirrels that year. Juvenile survival was the same on all plots in 1972 and 1973, with the exception of a better survival of juvenile males on plot 2. Also, treated adults never acted agonistically towards juveniles. However, levels of young-young agonistic behavior were the same on all plots in 1972. Juvenile survival was reduced on the control plot over the winter 1973-1974 while it remained the same on plots 2 and 3. These two plots were characterized by low densities in 1973, especially of their juvenile populations. Adult-young agonistic behavior was observed to be reduced on low density plots as compared to high density plots. Moreover, in juvenile populations of low density, juveniles did not interact agonistically with each other; they did so on higher density plots. Thus, generally the better survival of some groups of adults and juveniles was also associated with reduced densities and reduced levels of agonistic interactions.

Survival of adults was improved by treatment; treated squirrels did not breed, immerged earlier, were less aggressive than non-treated squirrels and survived better than the latter. In normal populations, harsher climatic conditions were more detrimental to the survival of some classes of squirrels than to others. However, the usual survival disadvantage of non-resident adults and juvenile males and females was reduced on the treated plots. Generally, for juveniles and treated adults, improvement in survival coincided with the reduction of agonistic behavior levels among these groups of squirrels. There was some indication that population density per se may affect survival; survival could be reduced as density increased.

2. Immigration of adults

Immigration of adults occurred in early spring before and during the establishment of territories or home areas by the local squirrel populations. Many adults moved onto the plots in March just after emergence from hibernation, as illustrated by the numbers of newcomers present in the early April populations. Other adults attempted to move onto the plots later on, when territories were being established. This immigration was the April-May immigration.

In late March and early April 1973 and 1974, the composition of the populations were known and comparisons could be made with the populations of the previous years. Such comparisons revealed that early immigrants represented from 38% to 60% of the early April 1973 populations, and that the largest proportion of newcomers was seen on plot 3, the plot with the lowest density in 1972 and 1973. Similarly, March immigrants represented from 0% to 17% of the populations in April 1974, but no difference could be seen between low and high density plots. This lack of difference was attributed to the population reduction brought about around plot 3 by the previous mestranol treatment and by mortality causes, so that very few squirrels were available to move in. Generally, proportions of newcomers were reduced in April 1974 as compared to April 1973. This was attributed to the lower survival of squirrels in 1973-1974, as determined by the harsher climatic conditions of the winter and spring 1974.

Immigration of adults onto the plots during April and early May was a function of the mestranol treatments given. No adult immigration was ever observed at that time on the non-treated plots, while it occurred on all treated plots. Immigration was higher on high density treated plots (plots 2, 1972 and 1973) than on a low density treated plot (plot 3-1972). This was attributed to the higher 'desirability' of plot 2 over plot 3, as illustrated 1. by the smaller size of core areas on plot 2, thus implying a better food supply, and 2. by the greater squirrel density seen on plot 2 in relation to the surrounding population. No such difference in density was seen on plot 3 and size of the core area was the greatest on that plot. The numbers of adult squirrels to move in during April and early May were thus determined by two opposite forces: 1. the opposition offered by the populations already present on the plots, which increased with density but decreased with treatment, and 2. the willingness of squirrels to move onto a given plot, according to the 'desirability' of that plot.

Adult immigration in April-May was also influenced by the food supply. Overall, April-May immigration was reduced in 1973 as compared to 1972. The food supply being better in 1973, it is likely that many areas that were marginal in 1972 were then able to support squirrels populations; thus plots would have lost some of their attractiveness to prospective immigrants.

Treated squirrels had reduced levels of agonistic behavior as compared to non-treated squirrels. Non-breeding females shared their core areas extensively with other squirrels presumably because they had only themselves to feed. Such core area overlap was almost non-existent for breeding females. It is such a change in behavior that may have allowed immigrant squirrels to move in and establish residency on the treated plots.

Overall, early adult immigration in March was greater on low density plots than on high density plots, when squirrels were available to move in. Immigration between April and early May occurred only on treated plots, and may have been a function of the 'desirability' of a given plot. Reduced levels of agonistic behavior for treated squirrels probably allowed adult immigration to take place since no immigration was ever observed between April and May on the non-treated plots. Low density plots generally attracted fewer immigrants, and an overall improvement of vegetation reduced the attractiveness of the plots to prospective immigrants.

3. Emigration/mortality and residency success of the adult populations

Maximum numbers of adults were observed on the plots between April and May each year when all the squirrels trapped in late March and the April-May immigrants were trying to establish residency. In early May, some of these squirrels were no longer observed within or near the plots; they had emigrated or were dead. Large proportions of the April populations were left on the plots in early May but only a portion of these succeeded in establishing territories. These squirrels formed the resident populations. The squirrels that were left over i.e. non-resident squirrels, either established residency nearby, or eventually drifted further away as they were no longer seen around the plots.

No difference in emigration/mortality of the adults between April and May was observed between any of the plots in 1972 or 1973. However, on plot 3, mortality and/or emigration was greater in 1973 than in 1972. This difference could have resulted from the fact that no treatment was given on plot 3 in 1973 in contrast to a 78% treatment in 1972; treatment was correlated with a reduced adult dispersal in 1972. Also, three resident adults were killed by badgers in 1973; such predation was not seen in 1972.

The mestranol treatment influenced the establishment of residency within a given plot. Proportionally more squirrels became resident on the treated plots than on the non-treated plots. Within a given plot, treated squirrels were more successful in establishing residency than non-treated squirrels (plot 2), as they seemed to be more tolerant of other squirrels and extensively shared their core areas. Increased success in establishing residency was also characteristic of the adults immigrating into the treated plots between April and May. None of the squirrels attempting to move into the non-treated plots succeeded in doing so. As a result of the increased immigration and overall greater success in establishing residency on the treated plots, populations on these plots either remained the same in April and May, or even increased their numbers. In no case were the decreases observed on the non-treated plots seen on the treated plots.

On the control plot, an increase in the number of resident squirrels was observed in 1973 coinciding with an increase in food supply. Concurrently, a decrease of adult female agonistic behavior was observed during the 10-day periods 1-4 (late April, May), during which time territories or home areas were established. This increase in squirrel numbers was not observed on plots 2 and 3 though. This failure to exploit the improved vegetation conditions observed in 1973 was generally due to a poor survival of the spring population on plot 3 and to a reduced April - May adult immigration on plot 2. Thus improvement of the food supply resulted in increased resident numbers only on the control plot in 1973.

Density affected the chances of establishing residency. In 1973, proportionally more squirrels became resident on plot 3 than on plot 1; both plots were left untreated but density was lower on plot 3.

Overall, treatment and low density resulted in a better chance of establishing residency probably as a result of the lower aggression characterizing treated squirrels and adults from low density populations. An improvement in food supply was followed by an increase in the resident population, but only when available squirrels were present around the plots to supplement the natural losses occurring on the plots themselves.

4. Natality

Natality was much reduced on the treated plots as the large majority of the treated females were sterilized during the year of the treatment, and produced smaller than average litters the following year.

Natality, as expressed by the size of emerging litters, was also a function of body weight, as related probably to the food supply available. Heavier females had larger emerging litters. This difference reflects the reproductive potential of these females as it was shown by Dorrance (1974) that heavier females have a higher rate of implantation. Juvenile mortality between birth and emergence is also related to the nutrition of the lactating females; a better food supply increases juvenile survival in the maternal burrow (Dorrance, 1974).

The size of the emerging litters was not greater in 1973 than in 1972, in spite of a better food supply in 1973. Smaller litters should be produced when the food supply is reduced (Lack, 1954). The correlate means that, within limits, an improved food supply should be characterized by larger litters. The lack of increase in the size of the emerging litters in 1973 could be explained partly 1. by the greater abundance of predators in 1973, and hence by a possibly increased predation on the litters while still in their mothers' burrows, and 2. by the fact that torrential rains may have drowned many juveniles that year. These effects were especially marked on plots 2 and 3 which were further from my trailer, thus were less protected from predators, and also because, contrary to what was observed on plot 1, very few juveniles had emerged on these plots when the torrential rains were observed. However, the effects of food supply increase were felt on the control plot. The size of emerging litters was not increased but more females established residency in 1973; as a result, more juveniles were born on that plot that year.

Natality was indirectly influenced by social behavior. On the treated plots, the reduced aggressiveness of treated squirrels allowed the immigration in April-May of non-treated adults, which were then able to reproduce within the limits of the plots. Normally, these squirrels would not have been able to do so, as no adult immigration ever took place onto the non-treated plots at that time of the year. However, no relationship could be established as such between natality and social behavior during this study. A relationship was established by Hoffman (1958) between natality as measured by ovulation rate, litter size and population density. No such relationship could be established either since the number of implantation sites was not recorded, and that factors such as predation largely influenced the size of emerging litters.

The main determinant of natality in a given plot was the food supply; heavier females produced larger litters, and generally population density was higher on plots with a better food supply. Treatment reduced natality as it successfully sterilized most females. However, this reduction of natality was compensated somewhat on the treated plots, since the reduced aggressiveness of the treated squirrels allowed immigrant squirrels to establish themselves on the plots and breed. No direct relationships could be established between population densities, levels of social behavior and natality during the present study. Predation and climatic conditions could affect the size of emerging litters to a great extent.

5. Dispersal/post-emergence mortality of juveniles

When sizable populations of juveniles were born on all plots, the pattern of decline of the juvenile populations was the same on treated and non-treated plots. At the end of the summer (1972) though, proportionally more juveniles remained on plot 3, a plot of lower density. This correlated with Dorrance's (1974) findings; after removing portions of Richardson's ground squirrels juvenile populations, he concluded that egress of juveniles was density related. This phenomenon was also observed in the Uinta ground squirrel (Balph, 1970). In 1973, no juvenile dispersal was observed on plot 3 although no treatment was given then, whereas it did occur plot 2. However, the fact that juvenile populations were reduced to a few individuals on these plots, allowed for large fluctuations in juvenile numbers which may not reflect the effect of reduced density as such.

Improvement of food supply in 1973 did not change the proportion of juveniles that emigrated or died on the control plot during that summer. However, more juveniles being born that year, more were left at the end of the summer with home burrows within the plot boundaries. The fact that juveniles had not started to hibernate yet at the end of August 1973, indicated that juvenile population on plot 1-1973 probably had not yet reached its lowest level. Thus it was impossible to compare the numbers of juveniles left on that plot at the end of the summers 1972 and 1973, and to measure the impact of the improved food supply and of the greater juvenile density on the rate of juvenile dispersal on that plot.

In 1972, levels of agonistic behavior among juveniles were the same on all plots. The fact that adult-young aggression was reduced on plot 3, both as a result of treatment and of the low population density, may explain the reduced juvenile dispersal observed on this plot. In 1973, no agonistic interactions took place between juveniles on plots 2 and 3 as born juveniles were very few. Adult-young agonistic encounters were significantly reduced (per adult) on plot 2 in 1973 as opposed to 1972. However, so few juveniles were present on plots 2 and 3 in 1973 that valid comparisons could not be made between social behavior and their dispersal. Levels of agonistic behavior were the same between adults and young and between young on plot 1 in 1972 and 1973. Although in 1973 the numbers of adults and juveniles were both increased in relation to 1972, the average numbers of active squirrels were the same each year. The proportions of juveniles to disperse on that plot (#1) were the same each year. In summary, no strong relationship could be established between the levels of agonistic behavior to which each juvenile was submitted on the part of adults or of other juvenile, and the rate of juvenile dispersal on any given plot, with the exception possibly of plot 3-1972. On that plot, both treatment and low density combined to reduce levels of adult-young agonistic behavior and possibly, the dispersal of juveniles. Similarly, Yeaton (1972) concluded that in Richardson's ground squirrels, no relationship exists between aggression and dispersal of juveniles.

Dispersal of juveniles accounted for large losses of squirrels in the populations. However, these losses did not seem to relate to the food supply nor to the levels of agonistic behavior observed on the plots. There was evidence that dispersal was reduced with decreasing densities.

6. Juvenile immigration

Juveniles did not immigrate in greater numbers onto the treated plots than onto the non-treated plots. This was expected however as the populations surrounding the treated plots were also reduced by treatment (plot 2-1973, plot 3-1972). No treatment was given around plot 2 in 1972. However, the females that normally would have given birth to prospective juvenile immigrants had moved into the plot itself in April and established residency. Their progeny were so to speak 'immigrating juveniles in utero'! This would explain the small numbers of juveniles that immigrated into the plot later that summer, since the surrounding population had been depleted by the egress of its adult females in favour of plot 2.

Immigrating juveniles represented larger proportions of the total juvenile populations found on the treated plots since the number of born juveniles were reduced on these plots. Immigrant juveniles moved very early onto the treated plots. On the non-treated plots, they immigrated mostly at the end of the summer when born juveniles were already beginning to go into hibernation, or when the born population had been decreased by dispersal and mortality.

Juvenile density was reduced on the treated plots, which may have allowed such an early influx of juveniles. Burns (1968) showed that in the Uinta ground squirrel, the proportion of immigrant juveniles was greater in low density areas than in high density areas. Adult squirrel density was not reduced by the treatment, but treated squirrels went into hibernation sooner than non-treated squirrels. Adult population was reduced on the treated plots when juveniles were beginning to increase their home range and to look for alternate home burrows. Thus reduced adult and juvenile densities may have contributed to a greater immigration of juveniles.

The improvement of the food supply in 1973 did not increase the number of juveniles immigrating onto the plots. Areas that were marginal in 1972 could now support juveniles and the incentive for juveniles to move onto the plots may have been reduced. So the numbers of juveniles to immigrate in 1973 were roughly the same as in 1972, in spite of the fact that numbers of juveniles born in the surrounding untreated populations, thus prospective immigrants, were greater in 1973.

Juveniles moving early into the treated or low density plots had good chances to establish a home burrow and to accumulate the weight necessary for a successful hibernation. Moreover, levels of agonistic behavior were reduced on these plots. Thus the juveniles moving into these populations probably had better chances of survival than juveniles moving into high density, non-treated plots. The juveniles moving into the latter plots were doing so late in the summer. They had no choice of 'good' home burrows. Furthermore, vegetation by that time had probably lost much of its nutritive value (Dasmann, 1966, p.63). On the other hand, by moving into the plots then, they may have been improving their chances of survival, presumably moving into a better habitat in comparison to the one they left.

I think that this earlier immigration was both a function of the lower numbers of adults and juveniles found on these plots at the time of juvenile dispersal, and of the lowered levels of agonistic behavior observed there. An improved food supply was not followed by an increased juvenile immigration. Most likely, surrounding areas were then able to support squirrel populations and the plots themselves became relatively less desirable.

D. Social Behavior

In the previous sections, social behavior was considered as one of the factors affecting the annual cycle and the population dynamics of the populations studied. I review here how social behavior itself was influenced by treatment, population density, changes in weather, food supply, etc.

1. Adult-adult behavior

Cohesive behavior among adults was rare and sporadic and was only observed between neighbours and related squirrels. No difference in levels of cohesive behavior could be seen in relation to treatment, or population density.

Agonistic behavior was prevalent among adult squirrels between the time of their emergence until about 25 days before their return into hibernation. Adult agonistic behavior was related to the attempts for males to secure breeding partners, and to the necessity for breeding females to secure an adequate burrow and food supply for themselves and their progeny.

A few adult males succeeded in immigrating and establishing residency on the treated plots. Such a phenomenon was never observed on the non-treated plots. These males moved in when breeding was over so that they had little chance to contribute that year's cohort of juveniles. However, by immigrating onto a desirable plot, they most likely increased their chances of survival and therefore their chances of breeding the following spring as suggested by Murray (1967).

Relationships were established between the breeding status of adult females, the importance of their food supply and their spatial distribution, indicating that the role of agonistic behavior may be to provide an area, more or less exclusive, that will offer protection and food for breeding females and their offspring. The following observations support such a suggestion:

a. Levels of agonistic behavior among breeding females dropped drastically within 10 days from juvenile emergence as the latter began feeding on vegetation. Females then spent more time feeding, and extended their home range. The juveniles fed mostly on their mothers' core areas, until they too extended their home range. But overall, after juvenile emergence, there seemed to be little attempt from the part of the adult females to secure an exclusive feeding area, hence there was a reduction in adult agonistic behavior. It was while females were pregnant and lactating that they were seen to be most aggressive towards other adults. They could then have been considered to be "defending" an area, although its use may not have been exclusive. However, the decrease of adult-adult agonistic behavior was concurrent with the onset of adult-young agonistic interactions indicating that breeding females still had a strong "attachment" to their home burrow and adjoining core area.

b. Breeding females had larger core areas on a low density plot (#3) than on high density plots. In the low density populations, core area increased without any obvious direct relationship with density itself. On the other hand, when squirrel density increased, core area size decreased. There was a minimum size of core area though which did not decrease with increasing population density. This lower limit was probably the minimum area necessary for a squirrel to feed itself and her litter in the case of a breeding female.

c. Breeding and non-breeding females on a same plot had equal sized core areas. However, breeding females did not share any of their core area when food supply was poor, and shared very little of it when food supply was better. Instead, the area being used in a given plot was extended. Similarly, in the round-tailed ground squirrel, greater crowding of squirrels means a greater clumping of core areas rather than an increase in the overlap of core areas (Dunford, 1977b).

d. An increase in resident densities was observed on plot 1 in 1973. Agonistic behavior was significantly reduced during the 10-day periods 1-4 (i.e. during late April and during May) when compared to the same period in 1972, and throughout the summer, levels of adult agonistic interactions were the same in 1973 as in 1972. Annual cycle data showed that in April and May, females were undergoing pregnancy and were lactating. I believe that such an increase in squirrel resident density, seen without a concurrent increase of adult agonistic behavior, was possibly a result of the better food supply present in April and May 1973. The average monthly temperature was slightly warmer during these two months in 1973 (40 F) than in 1972 (38 F), and more rain fell (2.15" in 1973 versus 1.54" in 1972) (Alberta Environment, 1972, 1973). These small differences may have triggered an earlier vegetation growth and allowed more females to establish residency without an undue increase of aggression. Christian (1970) postulated that there is probably an optimum degree of aggressiveness for a particular species, beyond which increases in aggressiveness may be incompatible with adequate reproduction and survival.

This lack of increase of agonistic behavior, in spite of an increase in density, may also result from changes in the social structure of the population. A more rigid social structure at higher density may lower fighting (Lloyd and Christian, 1967). In the Uinta ground squirrel, greater density appears to increase the social stability by limiting the amount of intrusion from non-residents, thus producing lower intensity of encounters (Morse, 1978).

e. Females that did not breed shared their core areas with males, breeding or non-breeding females alike, and their level of agonistic behavior was usually lower than for breeding females. The latter did not share their core area with other breeding females. The tolerance shown by treated squirrels may be comparable to the tolerance shown by subordinate adult males in populations of Columbian ground squirrels. In these populations, overlap of core areas is only 6% among dominant males, while subordinate males share 49% of their core area with dominant males. Moreover, as was observed during the present study between breeding and non-breeding females, in these populations the mean size of core areas is the same size for both groups of males (Murie and Harris, 1978).

That the core area was highly used by adult females in April and May, and served to protect the space and food necessary for reproduction was further illustrated by the large immigration observed on the treated plots. Sterilized squirrels were not breeding, and extensively shared their core areas. Immigrant adults were able to move in and breed. This suggests that the factor which was previously keeping these squirrels out was the intolerance of squirrels ready to breed rather than the food supply or the number of burrows available. In effect, adult immigration was characteristic of the treated plots only, and within a given year, immigration occurred while the numbers of burrows or food supply remained the same for a given plot.

Levels of adult agonistic behavior were higher on plots with a high population density than on low density plots when food supply was poor. Generally, higher density plots attracted more immigrants than low density plots. As such, a higher social pressure would be on the high density plots, as not only were there more squirrels within their boundaries, but also there was constant pressure from non-resident squirrels attempting to move in . This again was related to the necessity of securing an adequate food supply for successful breeding, since levels of agonistic behavior for treated squirrels did not change with increasing density. Such a relationship was also observed in the Uinta ground squirrel. During years of high population density, females exhibited higher frequencies of behavior that could be related to aggression than they did during years of low population density (Morse, 1978). Similary, in the same species, encounter rates among squirrels were higher on high density areas than in low density areas (Burns, 1968).

In the adult population, the function of agonistic behavior was closely related to the breeding status of squirrels and their ensuing energy requirements. Their spatial distribution reflected these needs. Core areas were larger in poorer habitat, thus densities of populations were lower there. Overlap of core areas among breeding females was very small in all plots, even when resident density was increased. Breeding females′ core areas never overlapped to the same extent as for non-breeding squirrels, which extensively shared their core areas with both breeding and non-breeding squirrels. Size of core area decreased with increasing density but never went below a minimum area which probably provides the essential requirements of space and food for an individual squirrel. Agonistic behavior may adjust the populations to their prevailing food supply, since in a year of poor food supply, the frequency of adult agonistic behavior was greater on the high density plots. However, such a relationship was not observed in a year of better food supply, when there was an increase of the resident density in a given population, without a concurrent increase of adult aggression.

2. Adult-young behavior

On the non-treated plots, most adult-young cohesive interactions took place between mother and offspring. On the treated plots, almost half the cohesive interactions occurred between juveniles and non-related adults. Most of these interactions took place when juveniles started moving away from the maternal burrow, but stopped within a month of juvenile emergence. This difference between plots is attributed partly to the reduction of aggressiveness of the treated squirrels. Treated squirrels were never seen to behave agonistically towards juveniles. However, when levels of adult-young agonistic behavior were compared for all squirrels between treated and non-treated plots no differences could be shown. Overall, juveniles were the subject of as much aggression from adults on the treated plots as on the non-treated plots, except when juvenile density was much reduced.

Adult-young agonistic behavior was also a function of population density. Within a given year, adult-young aggression on the part of breeding females was greater on a high density plot (#1-1973) than on a low density plot (#3-1973). Non-treated squirrels were significantly more aggressive towards juveniles than were the treated squirrels on a high density plot (#2-1972), while no difference occurred between these two groups on a low density plot (#3-1972). Moreover, a reduction in the number of juveniles born on a given plot saw a concurrent decrease in the number of agonistic acts to which each juvenile was submitted (plot 2, 1972 and 1973). Adult-young agonistic behavior on normal plots was related to the combined density of adult and juveniles (plots 4, 5, 6).

Levels of agonistic behavior as averaged over the summer were not the only factors that may have affected juveniles on the treated plots. Treated squirrels returned into hibernation sooner than breeding squirrels. Therefore, few adults were present on the treated plots when juveniles were increasing their home range. However, the partial absence of treated adults from the populations does not explain the total lack of aggression observed between themselves and the juveniles. Both groups were present at the same time on the plots for an average of 30 to 40 days each year. During that same period, agonistic interactions were common between non-treated adults and juveniles.

Improvement of the food supply did not increase or reduce the average numbers of adult-young agonistic interactions observed on the control plot in 1973. Numbers of adult residents were greater in 1973 and more juveniles were born, but no difference could be shown between 1972 and 1973 in the average numbers of active adults and juveniles. The fact that generally, adults returned into hibernation earlier in 1973 than in 1972 may have also contributed to the maintenance of the adult-young agonistic interactions at the previous year's level, in spite of increased population density. Since juveniles on average emerged at the same time in 1972 and 1973, by the time they started extending their home range in 1973, many adults had already hibernated, hence reducing the likelihood of adult-young agonistic interactions.

Only 15% of all agonistic interactions were observed between adults and juveniles. No difference could be shown between overall levels of adult-young interactions on the treated and non-treated plots. It appears that aggression from adults towards juveniles plays only a minor role in their dispersal, as is the case in the Uinta ground squirrel (Burns, 1968). However, the numbers of agonistic acts observed may not reflect the full impact of adult aggression towards juveniles. The experience for a juvenile of being attacked by an adult at an early age may be much more stressful than a similar attack by another juvenile. As such, the few adult-young agonistic interactions observed may be more meaningful than their numbers suggest. The fact that adult-young agonistic behavior increased with density suggests that such behavior should contribute to the control of the juvenile populations.

3. Young-young behavior

Cohesive behavior was very common among littermates during the first month following their emergence from the maternal burrow. As juveniles started to disperse and to extend their home range, cohesive behavior gradually decreased. In many plots, small numbers of young-young cohesive interactions were still observed at the end of the summer. In 1972, no difference could be shown between the control plot and the treated plots in that regard except for the fact that more interactions were observed between non-related juveniles on the treated plots than expected. This is possibly a consequence of the early juvenile immigration seen on these plots. Immigrant juveniles represented large proportions of the juvenile populations on the treated plots. Their parentage was not known since they came from outside the plots and it is possible that many of them could have been littermates, hence there was a greater than expected frequency of cohesive behavior between seemingly non-related juveniles on the treated plots.

In 1973, when juvenile populations were reduced to very small numbers on plots 2 and 3, cohesive interactions among juveniles were never observed. One of the reasons for this was that most litters on these plots included only 1 juvenile, or two at the most. Juveniles born on the plots, as well as immigrant juveniles, were well spread on the plots, thus their chances of encounter were much reduced in comparison to juveniles belonging to large litters.

Young-young agonistic encounters were common, representing 38% of all agonistic acts. Aggression between juveniles was observed within 10 to 20 days from their first emergence on all plots. No differences were seen in 1972 between the levels of young-young agonistic behavior observed on the treated and non-treated plots. However, the pattern of young-young agonistic behavior through the summer was different on the treated plots. While young-young agonistic interactions reached a high within a month on the control plot and them decreased, aggression was low on plots 2 and 3 during the first part of the summer and finally reached a plateau at the end of July and during the first part of August. This difference is associated with the nature of the juvenile populations present on the plots. During most of the summer, the juveniles present on the control plot were juveniles that were born on that plot. By contrast, immigrant juveniles moved early onto the treated plots and throughout the summer, represented large portions of the juvenile populations. The proportions represented by immigrant juveniles increased during the summer to stabilize 6-8 weeks after mean juvenile emergence on these plots. It is likely that the increasing young-young agonistic interactions observed on the treated plots could be the result of these further additions to the juvenile populations.

In 1973, no agonistic interactions were ever observed on plots 2 and 3 as both numbers of born juveniles and immigrants were very reduced. Juvenile density on plot 1 was high and so was the level of young-young agonistic interactions. Thus a greater juvenile density was characterized by a higher level of aggression among juveniles. This was corroborated by the observations made on plots 4, 5 and 6, where similar densities of active juveniles were characterized by similar levels of young-young agonistic interactions.

More resident females bred on the control plot in 1973 than in 1972 which meant that many more juveniles were born and remained as residents that year. However, the overall level of agonistic interactions observed between these juveniles in 1973 did not change in relation to 1972. Differences appeared though when the identity of the squirrels involved was considered. In 1972, most agonistic interactions were seen among non-related juveniles while in 1973, most interactions were observed among littermates. Moreover, most agonistic interactions took place between juveniles born on the plot, since immigrant juveniles represented only a small proportion of the population and moved in very late in the season, at which time juvenile aggression was much reduced. Michener (1973b) observed that usually yearling females inherit their mother's territory, or take up residency nearby; juvenile males do so only if their mother dies. Possibly in years of lower juvenile density, juvenile dispersal/mortality, as well as adult aggressive behavior, are enough to reduce the numbers of juveniles so that only one or two littermates are left at the maternal burrow when juveniles become aggressive to one another. In 1973, more juveniles were born and adults returned into hibernation sooner, so that the distribution of home burrows for juveniles probably had to be established mostly by the juveniles themselves. Since there is evidence that a female burrow is either retained by her or is transferred to her descendants (Yeaton, 1972), it is among the latter that most in-fighting should occur if juvenile population remains high in spite of predation, dispersal or mortality. The fact that many juveniles were born around the plot itself would have made dispersal more difficult in 1973 and predators were removed on plot 1 so when juveniles became aggressive to one another in 1973, it is likely that a larger number of littermates was left at each burrow hence the increased frequency of agonistic behavior among littermates.

No strong relationship could be shown between levels of young-young agonistic behavior and the densities of the juvenile populations. The only density related observation was that when juvenile density was reduced to only a few individuals, juveniles did not interact agonistically towards one another anymore.

An increase in the number of born juveniles on a given plot resulted in increased levels of agonistic behavior among littermates and reduced levels of interactions between non-related juveniles. Overall though, each juvenile did not initiate or was submitted to more or less agonistic interactions from other juveniles than during a year of lower juvenile density. Treatment, other than reducing the juvenile densities, seemingly had no influence on juvenile agonistic behavior.

E. Population regulation

During the present study, many factors were identified as contributing to the control of Richardson's ground squirrel populations. First, the control of the adult populations will be considered and then factors affecting juvenile populations will be discussed. The question will be asked whether social behavior does or does not regulate these populations.

ADULT POPULATION

Two major factors were seen as regulating the numbers present in the adult breeding population. First, each year on a non-treated plot, only one third of the adult squirrels succeeded in establishing residency and breeding within the plots' boundaries. The remaining two thirds either died or dispersed. Many of the unsuccessful squirrels established residency nearby and were seen again on the plots the following spring; others were never seen again. I attribute this large reduction in the numbers of squirrels on the plots at that time (April-May) to the social intolerance of the adult squirrels and especially of the adult females. This intolerance was in turn related to their breeding status since breeding females on high density plots were more aggressive than non-breeding females. Social intolerance was also related to density; breeding females were more aggressive on high density plots than on low density plots. Non-breeding females were unaffected by density in that regard; their levels of agonistic encounters did not change with increasing density. The fact that it was social intolerance, rather than the number of burrows or the food supply available that controlled the resident numbers within a given year, was indicated by the large April-May adult immigration observed on the treated plots each year. Although food supply and number of burrows did not change on these plots within a given year, squirrels were able to move in and survive well. This was never observed on the non-treated plots.

However the number of squirrels that could establish residency within a given year was also influenced by the food supply available that year, as food supply can change from year to year. In a year of poor food supply, competition was high during April and May to establish and maintain residency. In a year of better food supply, levels of agonistic behavior were decreased at that time and more squirrels could establish residency.

This was reflected in the spatial distribution of resident squirrels within the plots.

Secondly, mortality factors reduced the adult population. Mortality during the summer after residency was established, was low and appeared to be mainly due to predation. However, mortality between entry into and emergence out of hibernation was high, either as a result of predation by weasels or badgers on hibernating squirrels, but most likely as a result of starvation. Squirrels need to accumulate large amount of fats to survive through many months of hibernation. If they do not have enough reserves to last until spring weather allows emergence, they die (Michener, 1978). Although resident squirrels and treated squirrels were shown to have the highest survival rates, only a third of them survived between the time they were seen to enter hibernation in June each year, and the following spring.

These losses in the adult populations were compensated for by breeding; some of the juveniles would survive to be part of the adult population the following spring. Also adult immigration in early spring compensated for many losses. On a low density plot, as many as 60% of the squirrels found in early spring were immigrants. The latter represented lower proportions on denser plots.

In summary, the numbers of adults present within a given population, were severely curtailed twice a year. First, the number of squirrels present in the early spring population was reduced by as much as two thirds while squirrels established residency. This reduction in numbers was mediated through social agonistic behavior but could be adjusted to prevailing food supply conditions. Secondly, mortality factors, and especially overwinter mortality, further reduced the number of adults that had hibernated on the plots. Breeding and adult immigration were the factors that compensated for these losses and renewed the pool from which the adult population could be established each spring.

JUVENILE POPULATION

Regulation of the juvenile population was partly achieved through the same factors that governed the adult population since the size of the breeding population ultimately determined the number of juveniles that could be born. But other factors influenced the juvenile population itself.

The size of emerging litters was consistently lower on plots where females had smaller body weight. Since direct correlation exists between body size and biomass of vegetation (Dorrance, 1974), these smaller litter sizes may have been the result of a 'poorer' food supply on these plots. Predation and weather could have also influenced the size of emerging litters; I believe that as a result of these combined factors, that many litters were totally destroyed in 1973, while others were reduced significantly.

Social aggression did not seem to play as important a role in the regulation of juvenile populations as it did for the adult population. In the control plot each year, young-young, and adult-young agonistic interactions became frequent only a month after the first emergence of the juveniles in these populations. By that time each year, at least 30% to 40% of the emerging juveniles had already dissappeared from the plots either as a result of dispersal or of mortality. The remaining juveniles were those that were mostly involved in fighting with adults or other juveniles. Most of this fighting seemed to result from the fact that juveniles were then expanding their home range and contacting non-related adults or juveniles.

However, both the rate of juvenile dispersal, and of juvenile agonistic encounters with other juveniles or with adults were affected by density, indicating that social aggression may have provided a safety mechanism for regulating juvenile populations if dispersal or mortality had not already done so. Dispersal was greater in high density populations. The levels of adult-young and young-young agonistic encounters were also much greater in high density populations than in populations where the juvenile cohort was very small. Interestingly, in very high juvenile density, most agonistic interactions took place between littermates indicating that the purpose of this fighting may have been related to the 'inheritance' of the maternal burrow or core area. In Richardson's ground squirrel, burrows are usually transmitted from mother to daughter (Michener and Michener, 1973). Immigration of juveniles was also more important in the populations where the juvenile numbers had been reduced either as a result of treatment or mortality during the summer.

Overwinter mortality further reduced the juvenile populations left at the end of the summer. On average, in the control population, roughly 25% of the juveniles born each year were left with a home burrow at the end of the summer and few immigrant juveniles succeeded in establishing residency. Only 20% of these 'resident' juveniles survived to the following spring during a long cold winter.

On an annual basis, dispersal, summer mortality and overwinter mortality accounted for the loss of 80% to 90% of the juvenile populations born on the plots. Dispersal and summer mortality accounted for at least 50% of these losses in a given population and overwinter mortality was the second most important factor of reduction. There was some indication that social aggression may have contributed to the dispersal of juvenile and possibly affected their survival, especially in juvenile populations of high density.

AGONISTIC BEHAVIOR AND POPULATION REGULATION

Many compensation mechanisms were at work in the adult and juvenile populations to alleviate the decreases brought by treatment or other mortality causes. Decreased dispersal of adults and juveniles, increased immigration rate of adults and juveniles, and decreased annual mortality of adults and juveniles were all observed in treated or low density populations. These phenomena all coincided with a decrease in agonistic behavior frequency on the part of treated or non-treated adults towards juveniles or other adults. Such compensatory mechanisms were also observed by Slade and Balph (1974) in populations of Uinta ground squirrels that were reduced to half their previous density.

In the juvenile populations, social behavior may not have played as important a role as in the adult populations. Agonistic behavior did vary in relation to combined densities of adults and juveniles, but was considered to be important only when levels of juveniles reached unusually high levels of density. It was only then that agonistic behavior as such may have acted as a possible control of juvenile populations. Dispersal and mortality factors probably reduced the juvenile populations to a level where control by agonistic behavior was not necessary. On the other hand, agonistic behavior among adults was observed at moderate levels even in low density plots, since the levels of agonistic behavior on these plots were the same as in high density plots in a year of good food supply. Therefore, I assume that agonistic behavior contributes to the regulation of adult populations, both at low and high levels of population density. In the juvenile population, agonistic behavior may play a secondary role and affect juvenile dispersal, immigration or survival only when densities are high.

In order to decide if a given factor regulates a population, necessary and sufficient conditions must be fulfilled (Chitty, 1967). Watson and Moss (1970) detailed the conditions which would show that socially-induced mortality (or decrease in recruitment) limits breeding populations. These are:

A. (a) A substantial part of the population does not breed, either because animals die; or because they attempt to breed but they and/or their young die; or because they are inhibited from breeding even though they survive and may breed in later years.

(b) Such non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e. breeding) animals are removed.

(c) The breeding animals are not completely using up some resource, such as food, space or nest sites. If they are, the resource itself is limiting.

(d) The mortality (or depressed recruitment) due to the limiting factor(s) changes, (di) in an opposite sense to, and (dii) at the same rate as other causes of mortality (or depressed recruitment).

B. In addition, condition (e) is that numbers change following changes in food. This will show that food and behavior are both limiting, if (a), (b), (c) and (d) are also met.

Up to two thirds of the adult squirrels observed on the plots each spring were unable to establish residency and eventually left the plots' populations. Their fate was not known in detail. Some were seen to establish home burrows in nearby, sub-optimal areas, while others were never observed in the area again. A home burrow and a sufficient area to feed on are essential if a squirrel is to survive and to breed. No doubt some of the squirrels that moved out eventually found a home area, although it may not have been as good as the one they were originally attempting to obtain. However, squirrels that wander afield in early spring would be very vulnerable to predators. They would not have the protection offered by a colonial system and the familiarity of a known home burrow. Squirrels dash for a known burrow when afraid and will go down without any hesitation. I have seen squirrels bounce off dirt or some other object I had used to block their burrow entrances while attempting to trap them at another burrow.

Food supply is scarce in early spring and dispersing squirrels would expend much energy wandering around in search of a suitable area to settle in. Moreover, they would be subjected to much aggression on the part of resident squirrels as was illustrated by the fate of the few squirrels attempting to move into the control populations. If they succeeded eventually in finding a home area and breeding, their litters would likely be small since they may have to settle in areas of poor food supply. The number of implantations, and post-birth survival of juveniles are correlated with the vegetation biomass (Dorrance, 1974). If breeding occurred at all for these individuals, the number of juveniles they produced must have been reduced. The fact that social intolerance may result in the death of some individuals was illustrated by the fact that in a year of poor weather conditions, overwinter mortality on high density plots was greater for non-resident than for resident adults. Thus if a squirrel was not able to establish residency in a highly 'desirable' location, this would reduce its chance of survival. This situation would occur most likely in years of very high squirrel density or in years of very poor weather conditions when the possession of a 'sub-optimal' burrow could mean death. I believe that recruitment can be reduced for a substantial part of the population because many squirrel can die as a result of not finding a suitable home area or else, they will breed, but will do so in sub-optimal areas and produce smaller than average litters. In her study area, Wehrell (1973) indicated that while most of the females occupying the central area of a Richardson's ground squirrel colony bred and raised a litter, only a smaller proportion of the females occupying the periphery of the colony were as successful.

No dominant or territorial animals were removed here, but sterilization reduced the energy requirement of some of the squirrels and as a result they became socially more tolerant. Many adults subsequently immigrated into the treated plots; every immigrating female raised a litter. Thus the squirrels that normally were kept out of the plot populations were all physiologically capable of breeding.

The resources on the plots were not all used up either, as was again demonstrated by the large adult immigration observed on plot 2, a plot of initial high population density. The survival of these 'denser' than normal populations was not decreased either since it was similar to that observed on a non-treated plot of equivalent density.

The fourth condition (d), i.e. "mortality (or depressed recruitment) due to the limiting factor(s), changes in an opposite sense to, and at the same rate as other causes of mortality", was also fulfilled. All the compensatory factors operating in the treated populations were proof of this. Lowered aggression in a given plot was observed concurrently with decreased dispersal, increased immigration, and decreased mortality of adults and juveniles. However, the rates themselves were not always proportional to the intensity of the changes in behavior, since food supply affected them. For example, immigration was not the greatest on plot 3, although this plot was characterized by the lowest levels of aggression among some of its squirrel members. Generally though, lower aggression was concurrent with lower dispersal, higher immigration and higher survival.

Finally, the last condition, i.e. changes in numbers following a change in food supply, was also observed in the populations studied here. This was especially obvious in the control population in 1973 where adult resident population and number of born juveniles were both increased, seemingly as a result of improved vegetation conditions.

Therefore, I suggest that social behavior, as expressed through agonistic interactions between population members, contributes to the control of populations of ground squirrels at certain times, adjust them to the existing food supply, and therefore prevents them from over-exploiting their resources. Such social mechanisms were at work in the low and high density populations of adult squirrels, but seemed to be necessary for the control of juvenile populations only when all other factors of population reduction had failed to appreciably reduce their numbers.

F. Mestranol as a control technique for populations of ground squirrels

Mestranol effectively sterilized all but one of the females treated in 1972, and in the latter case resulted in the production of a single young in the emerging litter. Mestranol was possibly still affecting the reproduction of the treated females a year after the initial treatment, since these failed to produce normal size litters in 1973.

The productivity of a treated plot was drastically reduced by the treatment due to the sterilization of the resident females. However, many factors were seen to be at work, compensating for such losses. Immigration of breeding adult squirrels took place on the treated plots in early summer, a phenomenon not observed on the non-treated plots, and proportionally more of the squirrels present became residents on the treated plots compared to the non-treated plots. As a result, adults not previously present on the plots bred and produced litters that normally would not have been born in these populations. Treated adults survived better than non-treated adults, and thus more squirrels than expected were present the year following the mestranol treatment. Compensation also occurred in the juvenile populations. In populations of low juvenile density, juvenile dispersal was lower and annual survival of juveniles was greater in a year of harsh climate than on high density, non-treated plots. Moreover, juvenile immigration took place early into treated or low density populations, allowing foreign juveniles to establish a home burrow and to increase their chance of survival.

The compensating factors successfully replenished the treated populations during the first season, as the proportion of juveniles left in these populations in August 1972 was equivalent to that observed in the control population. However, one year following the treatment, i.e. at the subsequent emergence from hibernation in April 1973, the adult populations observed on the previously treated plots were reduced by about 40% in comparison to the numbers of adults present then in the control population. Fewer squirrels, or the same number of squirrels as observed the previous year, established residency in the treated populations in 1973, while the number of residents significantly increased in the control population, likely as a result of improved vegetation conditions. A repeated treatment in one of the previously treated plots, and possibly an increased pre-emergence mortality of the juveniles on both plots, drastically reduced the number of juveniles emerging on plots 2 and 3 in 1973. Juveniles immigrated early into the treated populations in 1973 too, but failed to compensate for the large losses incurred. At the end of the summer 1973, the juvenile populations on the previously treated plots were only one fourth or one half of the numbers present at the same time the previous year; they represented only small fractions of the juvenile population present then on the control plot. In April 1974, two years after the initial treatment, only 30% (in a low density plot treated once at 80%) and 45% (in a high density plot treated twice, first at 50% and subsequently at 90%) of the original number of adults were left on the treated plots, whereas the control plot still retained 75% of its initial population.

The treated populations had the capacity to compensate to a certain extent for the losses incurred through natural reduction factors such as predation, bad weather, etc. However, the treatment put an additional strain on their ability to do so, and when high natural losses occurred, or in the face of a repeated treatment, these populations noticeably dropped. Treatment was given around the treated plots as well but in no instance was treatment applied further than 100 meters from the plots' boundaries. One of the compensatory mechanisms allowing treated populations to alleviate the losses resulting from the treatment was the increased immigration rates of adults and juveniles into these populations. Such a compensatory factor would most likely be eliminated if treatment was given over a much larger area, so that only improved survival and residency success of adults and juveniles would still be compensating for the population reduction due to treatment. Given the population reductions observed during the present study, and assuming the applicability of a control program over a much larger area, it is suggested that populations of Richardson's ground squirrels could successfully be reduced to much lower levels of population with the use of a chemosterilant. A total extermination of these populations is unlikely though as the success rate of a bait application would probably not reach the treatment rate applied during the present study. Thus the application of sterilizing baits would have to be repeated, possibly in alternate years, to appreciably affect these populations. Also, different doses of mestranol, or another chemosterilant, should be experimented with so that permanent sterility of the treated squirrels can be achieved if desired.

SUMMARY AND CONCLUSIONS

In April 1972 and 1973, different proportions of Richardson's ground squirrel populations were treated with mestranol, a chemosterilant that sterilized all but one of the females treated. Over a 2 year study, comparisons were made between treated and non-treated squirrels, and between treated and non-treated populations. The conclusions reached during this study will be summarized in a point by point form and will be concerned with 1. the annual cycle, 2. the population dynamics and 3. the social behavior of the populations involved. Conclusions regarding possible means of 4. population regulation will be given and 5. the potential of mestranol as a control agent will be assessed.

ANNUAL CYCLE

1. The spring emergence from hibernation and the breeding of adult squirrels was determined primarily by the spring climatic conditions; cold temperature and the slow melting of the snow cover postponed emergence and hence breeding.
2. The timing of adult breeding and of juvenile emergence could have been influenced by the food supply on a given plot, as mediated through the body weight of the females occupying the area. Heavier females bred earlier.
3. Onset of hibernation was determined by a squirrel's weight and weight increase as influenced by its breeding status, age, sex, and by the food supply available to this squirrel. High population density and high levels of social aggression both contributed to delay the onset of hibernation.

POPULATION DYNAMICS

4. Annual survival of sterilized adult squirrels was improved in comparison to that of non-treated, breeding squirrels. Non-breeding squirrels were able to accumulate fat faster than breeding squirrels, and hibernated earlier.

5. Annual survival of juveniles, both females and males, was improved in the treated populations possibly as a result of the lowered levels of aggression and lowered juvenile densities observed in these populations.
6. Annual survival of non-resident adults was equal to resident survival in a low density population, in a year of poor winter and spring weather conditions. In high density populations, residents survived better than non-residents given the same weather conditions.
7. In early spring, more adult squirrels immigrated into low density populations than into high density populations.
8. Adult immigration in early summer was observed only in treated populations, possibly as a result of the lowered levels of agonistic behavior characterizing treated adults.
9. Proportionally more adult squirrels established territories in low density and in treated populations, possibly a result of the lower levels of agonistic interactions observed among some groups of squirrels in these populations. An improvement in food supply allowed an increase in the number of adult squirrels establishing residency in a given population, without a concurrent increase of agonistic behavior.
10. Natality was drastically reduced by the treatment as most females were sterilized by a 1 mg dose of mestranol. Natality, as measured by the size of the emerging litters, may have been influenced by the food supply available to breeding females. Heavier females consistently had larger emerging litters. Predation and climatic conditions could also have influenced the size of emerging litters to a large extent during a given season.
11. Juvenile dispersal/post-emergence mortality was density related; proportionally less juveniles dispersed or died in low density populations. Dispersal and/or mortality accounted for nearly half of the annual juvenile losses observed in the control populations.
12. Non-resident juveniles immigrated earlier into treated and low density populations, and represented larger proportions of the total juvenile cohorts in these populations. This may have been related to the reduced juvenile and adult densities, as well as to the lower levels of aggression observed between adults and juveniles, and between juveniles themselves in these populations.

SOCIAL BEHAVIOR

13. Adult agonistic behavior was directly related to the breeding status, and thus metabolic demands, of the adult squirrels. Breeding individuals were more aggressive than non-breeding ones. Moreover, core areas of breeding females rarely overlapped, whereas overlap was extensive for non-breeding females.
14. Breeding squirrels were more agonistic in high density populations than in low density populations. The levels of agonistic behavior for non-breeding squirrels did not change with density.
15. An improvement in food supply allowed an increase of adult resident density without a concurrent increase of agonistic behavior among the residents.
16. Adult-young agonistic interactions increased with rising population density and may have contributed to the dispersal of the juvenile populations. Non-breeding adults never behaved agonistically towards juveniles, indicating that the greater energy demands of breeding squirrels promote agonistic behavior not only towards adults, but also towards non-related juveniles.
17. In very low density populations of juveniles, young-young agonistic interactions were not observed. At intermediate density, juvenile agonistic behavior was common and was observed mostly between non-related juveniles. At the highest density of juvenile populations, agonistic interactions were numerous and occurred mostly among littermates. No strong relationship could be shown between levels of juvenile agonistic behavior and juvenile dispersal.

POPULATION REGULATION

18. Adult populations were probably regulated primarily by the social intolerance of the adults themselves when establishing residency , since as many as two thirds of the adults moved out of control populations in the spring. By contrast, reduced adult aggression in the treated populations allowed all squirrels to remain and immigrants to move in. Overwinter mortaltiy could also account for large losses. The number of adults able to establish residency was also a function of the food supply available.

19. The number of born juveniles was determined primarily by the numbers of adults breeding in a given population. Juvenile numbers were later reduced, first by pre-emergence mortality probably due to predation, or inclement weather, and secondly by juvenile dispersal or post-emergence mortality which accounted for as much as 50% of the juvenile losses during the summer. Over-winter mortality could further reduce juvenile numbers accounting for as much as half of the losses in a year of poor survival conditions.
20. Social behavior, as expressed by the numbers of agonistic interactions observed among squirrels, was involved in regulating adult populations, both at high and low levels of population density, and may also have contributed to the regulation of juvenile populations, although not to the extent it did in the adult populations.

POPULATION CONTROL

21. Mestranol treatment was considered to be a potential means of controlling populations of ground squirrels. However, a safe method to distribute an acceptable bait to the adult squirrels prior to breeding in early spring is needed. Moreover, the treatment would be more effective if squirrels accepted a bait (with a chemosterilant) that would permanently sterilize them.

Appendix 1. List of plants collected in the Youngstown area, within the plot boundaries and in nearby fields.

GRASSES
Agropyron spp. Wheat grass
Agrostis scabra Willd. Rough hair grass
Bouteloua gracillis. Blue grama
Bromus inermis Leyss. Brome grass
Calamagrostis montanensis Scribn. Plain reed grass
Hordeum jubatum L. Foxtail barley
Koeleria cristata (L.) Pers. June grass
Poa spp. Blue grass
Stipa sparea Trin. var. *curtisea* Hitchc. Porcupine grass

WEEDS
Axyris amaranthoides L. Russian pigweed
Chenopodium album L. Lamb's quarters
Lappula echinata Gilib. Bluebur
Polygonum convolvulus L. Wild buckwheat
Salsola kali var. *tenuifolia* Tausch. Russian thistle
Thalspi arvense L. Stinkweed

NATIVE AND INTRODUCED PLANTS
Achillea millefolium L. Yarrow
Antennaria spp. Everlasting
Artemisia ludoviciana Nutt. White Sage
Artemisia frigida Willd. Pasture sage
Atriplex nuttuallii. Atriplex
Cleome serrulata
Compositae (not identified for genus and species)
Descurainia richardsonii (Sweet) E. Schulz. Gray tansy mustard
Gaillardia aristata Pursh. Brown-eyed Susan
Grindelia squarrosa (Purch) Dunal. Gumweed
Gutierrezia sarothrae
Monolepis nuttalliana
Opuntia polyacantha. Prickly pear
Potentilla spp. Cinquefoil
Solanum trifolium. Three-flowered night shade
Solidago spp. Goldenrod
Symphoricarpos occidentalis Hook. Western snowberry

OTHER PLANTS (not found on the plot but
characteristic of the area)
Anemone patens var. *wolgangiana*. Prairie crocus
Malva sp. Scarlet mallow
Populus tremuloides Michx. Aspen
Potentilla fructicosa. Shrubby cinquefoil
Ranunculus rhomboideus Goldie. Prairie buttercup
Rosa acicularis. Prickly rose
Salix spp. Willow
Slyrinchium mentanum. Blue-eyed grass
Taraxacum officinale. Common dandelion
Thermopsi thombifolia. Golden bean

Appendix 2. List of the 45-minute observation periods made during the 1972 and 1973 seasons in plots 1, 2, 3, 4, 5 and 6: date, time of the day and weather.

10-day period	DATE	TIME PLOT 1	PLOT 2	PLOT 3	PLOT 4	PLOT 5	PLOT 6	WEATHER Max.	Min.	Others
1972	April									
	21	14:30	15:30	16:00				62	28	R;w5
	23	11:00	15:00					51	26	S;w3
	25	16:00	15:00	10:15				56	42	R;w4-5
1	26	10:45	11:30	14:30				64	27	S;w2
	27	9:45	13:00	11:30				72	28	S;w0-3
	28	14:30	17:15	15:30				80	41	S;w3-4
	29			10:30				62	34	Sn;w4-5
	May									
	1	17:00	16:00	15:00				60	30	S;w1-2
	2	9:30	8:00	11:00				64	25	S;w3
2	6	10:45						56	32	C;w2
	8	16:15	14:15	15:15				62	24	S;w3-4
	9	13:00	10:15	14:30				64	30	R;w3-4
	10	14:00	15:45	17:00				77	32	S;w1-2
	11	11:00	14:45	16:00				72	32	C;S;w1
	14	14.30	15.30	17.45				78	50	S;w1
	16	11:45						68	42	C;w1-2
3	18	15:45	11:15	10:30				70	40	S;w1-2
	19	15:30	12:00	11:00				-	44	R;w3
	20	13:15	10:15	11:15				-	-	w3-4
	22	16:15	11:15	13:45				72	42	C;S;w3
	23	15:15	11:00	14:00				68	42	S;w2
4	24	10:30	14:00	15:15				64	48	R;w2
	25	11:00	14:30	13:30				62	52	C;w1
	28	10:00	14:30	15:30				78	54	C;S;w1-2
	June									
	2	10:30	14:30	15:30				80	54	S;w1
	3	17:15	16:00	15:00				84	50	S;w1
5	5	16:30	10:15	14:15				84	49	S;w1
	6	10:30	9:30	8:45				89	50	S;w1
	7	13:30	10:00	11:00				93	59	R;S;w2
	11	15:30	14:30	13:30				78	60	S;w4-5
	14	15:00	13:45	16:30				66	48	C;w2
6	15	15:00	15:45					80	46	C;w2
	16	11:30	9:00	10:00				-	62	R;w2
	19	14:45	13:30	16:00				74	34	S;w1
	23			10:30				74	52	R;S;w2
	26	12:15	11:00	10:15				72	52	R;S;w2
7	27	11:00	10:00	13:30				70	44	C;S;w1-2
	28	10:45	13:45	11:45				84	44	S;w2
	July									
	13	10:45	11:45	12:45				79	56	R;S;w1-2
	14	11:30	12:45	13:45				74	53	S;w3
9	15	13:00	10:15	11:15				76	50	S;w2-3
	17	12:15	13:15	14:00				70	50	C;S;w2-3
	19	11:00	13:00	12:00				70	42	R;S;w1-3
	20	11:30	12:30	10:00				76	40	S;w0

	23	12:30	10:30	11:15				72	50	S;w2
	24	13:30	11:30	12:30				84	57	R;S;w3-4
	26	12:45	11:45	13:45				78	58	S;C;w0-1
10	27	16:00	14:00	15:00				82	56	R;S;w2
	28	9:30	11:30	10:30				84	56	S;w1-2
	29	10:30	9:30	11:30				76	52	S;w2-3
	August									
	1	10:30	12:15	11:30				68	52	S;C;w3
	3	12:30	11:30	13:30				80	42	S;w1-2
	4	11:15	12:15	10:15				84	48	R;S;w0
11	6	13:15	11:15					84	60	R;S;w2
	11	12:15						87	58	R;S;w0
	12	15:30	16:45	17:30				78	58	S;C;w0

1973	**April**									
	16	11:30	15:45	14:45				51	23	S;C;w1-2
0	17	9:15	10:30	11:15				53	27	S;C;w2
	19	15:30	12:30	13:30				49	32	C;R;w3-4
	21	15:00	12:00	13:00				52	32	C;S;w4-5
1	22	14:30	13:30	15:30				56	31	C;S;w1
	25	13:30	14:45	15:30				52	34	S;w2
	May									
	3		15:00					60	40	S;R;w2-3
2	4	12:00		10:30				54	36	S;w2
	5		10:30					50	32	S;w3
	9	10:45	9:45	11:30				52	46	C;R;w3-4
	11	12:30	11:30	14:00				56	22	S;C;w3-4
	13	11:30	10:15					66	32	S;w2-3
	14	11:15	10:00					72	32	S;w2-3
3	15			10:15				77	36	S;w2
	19		11:30	12:30				60	44	S;C;R;w3
	20	11:00						60	38	C;S;w3
	21		9:15	11:00				78	32	S;w1
	25	10:45						64	44	S;w4
4	29	10:00	17:00	17:45				70	43	C;R;w2
	30	17:00	11:00	10:00				78	46	C;w3-4
1973	**June**									
	2	12:00			15:30	12:00	16:30	62	31	S;w2
5	4		10:00	9:00				64	39	S;w4
	8		14:00		10:00		11:00	72	34	S;C;w2-3
	9	16:45		15:30				68	42	S;C;R;w1
	13				12:00	11:00	10:15	82	44	C;S;w2
	17	11:00						62	44	R;w3
6	19	10:30			11:30	14:15		64	48	S;R;w2-5
	20		11:15	14:30			14:15	74	48	S;w2
	23	10:15		10:00	17:00	11:15	17:15	82	57	S;w2
7	29	15:00			14:00	11:15	12:00	72	54	S;R;w2
	30	14:15			11:15	10:15	13:15	70	55	C;w2

	July									
	2	16:00			14:45	10:00	10:45	73	50	S;w2
	3					10:30	11:30	80	50	S;w1-2
8	4	16:30			10:00			85	55	S;C;w3
	6				14:15	11:45		71	56	R;C;S;w1-2
	8						10:15	80	50	S;w1
	10	14:30					11:45	90	55	S;w2-6
	14				11:00			83	46	S;w1
9	16	16:00				11:30	10:15	72	52	S;C;w3-4
	18				9:45	10:30		70	50	S;R;w1-3
	19	8:45				12:00	10:15	75	46	C;S;w1
	August									
	5					10:45	11:30	93	58	S;w1-2
11	8	15:15						76	55	S;C;w0-1
	9	17:00			10:30	16:00	11:15	84	55	S;w0-1
	10	9:30			10:30	11:30	14:30	82	58	S;R;w0-1
	11				15:30			82	57	C;S;w1
	13	16:30	11:30	12:00	17:30			86	60	S;w2
	14					9:30	10:30	85	59	S;w1
12	15	17:00						86	55	S;w1-3
	16				11:45	17:30	16:30	80	55	S;w1
	17	9:45			13:45	10:45	14:30	74	52	S;w1
	26	13:45			10:30	11:00	16:15	76	46	S;w2-3
13	27	9:00			11:30	10:30	9:45	75	50	S;R;w1-5
	28	12:00	13:00	14:00	9:45	10:30	11:15	74	43	S;R;w1-3

Max.,Min. : maximum and minimum temperature(F);
R: rain; S: sunny; C: cloudy; Sn: snowing
w0 : no wind; w1 : 0-10 miles per hour(mph); w2 : 10-20; w3 : 20-30;
w4 : 30-40; w5 : 40-50; w5 : 50-60

Appendix 3. Total number of cohesive interactions observed on plots 1, 2, 3, 4, 5 and 6 during 1972 and 1973.

	GROUPS OF SQUIRRELS INTERACTING									
	ADULT-ADULT				ADULT-YOUNG			YOUNG-YOUNG		ALL SQUIRRELS
	AA	AM	MA	MM	AY	MY	AownY	YY	Litt.	
1972										
plot 1 *54	3	-	-	-	9	-	27	10	38	87
plot 2 *51	1	3	0	1	8	3	29	13	53	111
plot 3 *50	0	0	1	0	3	4	5	9	8	30
1973										
plot 1 *36	0	-	-	-	2	-	30	0	74	106
plot 2 *21	1	0	1	2	2	1	4	0	3	14
plot 3 *21	0	-	-	-	0	-	5	0	0	5
plot 4 *21	0	-	-	-	11	-	?	39	?	50
plot 5 *21	0	-	-	-	7	-	-	41	?	48
plot 6 *22	2	-	-	-	31	-	-	54	?	87

* : number of 45-minute observation periods made.
\- : these groups of squirrels were not present.
? : the relationships between squirrels were not known.

Appendix 4. Total number of agonistic interactions observed on plots 1, 2, 3, 4, 5 and 6 during 1972 and 1973.

	GROUPS OF SQUIRRELS INTERACTING									ALL SQUIRRELS
	ADULT-ADULT				ADULT-YOUNG			YOUNG-YOUNG		
	AA	AM	MA	MM	AY	MY	AownY	YY	Litt.	
1972										
plot 1 *54	211	-	-	-	56(4)	-	0	111	27	405
plot 2 *51	71	22	14	4	60(5)	0	1	119	25	316
plot 3 *50	9	10	15	10	11(4)	0	0	48	9	112
1973										
plot 1 *36	59	-	-	-	43(13)	-	0	0	119	221
plot 2 *21	27	10	22	29	5	0	0	0	0	93
plot 3 *21	49	-	-	-	1	-	0	0	0	50
plot 4 *21	5	-	-	-	10	-	?	117	?	132
plot 5 *21	6	-	-	-	30	-	?	112	?	148
plot 6 *22	15	-	-	-	69	-	?	113	?	197

( ): Number of AY interactions won by juveniles. These are included in the number given under the AY column.
* : Number of 45-minute observation periods made.
\- : These groups of squirrels were not present.
? : The relationships between squirrels were not known.

Appendix 5A. Average numbers of ground squirrels observed during a 45-minute observation period for all 10-day periods in plots 1, 2 and 3 during the 1972 season.

1972 10-day period	PLOT 1 (0.65 ha)		PLOT 2 (0.69 ha)			PLOT 3 (0.81 ha)		
	A	Y	A	M	Y	A	M	Y
1	19.0 *6	-	11.0 *6	5.2	-	3.3 *6	6.2	-
2	14.8 *5	0.8	9.3 *5	6.3	-	4.6 *5	5.4	-
3	10.3 *6	14.5	8.0 *5	5.8	3.0	3.5 *5	4.7	1.0
4	14.0 *5	18.8	10.4 *5	6.6	9.8	3.1 *5	5.7	1.8
5	7.6 *5	16.6	9.9 *5	4.6	20.6	2.3 *5	3.7	4.8
6	4.8 *5	15.4	8.0 *5	1.7	21.4	3.3 *5	0.7	8.3
7	- *3	19.3	4.7 *3	-	24.0	2.3 *5	-	10.3
9	- *6	17.3	1.7 *6	-	16.0	- *6	-	10.2
10	- *6	16.2	0.8 *6	-	21.8	- *6	-	13.0
11	- *5	15.8	- *5	-	21.0	- *5	-	8.6

* : number of 45-minute observation periods made during a 10-day observation period.

NO : no observations were made

Appendix 5B. Average numbers of ground squirrels observed during a 45-minute observation period for all 10-day periods in plots 1, 2, 3, 4, 5 and 6 during 1973.

1973 10-day period	PLOT 1 (0.65 ha)		PLOT 2 (0.69 ha)			PLOT 3 (0.81 ha)		PLOT 4 (0.40 ha)		PLOT 5 (0.40 ha)		PLOT 6 (0.40 ha)	
	A	Y	A	M	Y	A	Y	A	Y	A	Y	A	Y
0	24.7 *3	-	11.0 *3	7.0	-	15.0 *3	-						
1	22.0 *3	-	12.3 *3	7.0	-	12.0 *3	-						
2	19.5 *2	-	9.3 *3	6.7	-	8.0 *2	-						
3	17.8 *4	14.7	9.0 *4	6.5	0.2	8.0 *4	-						
4	6.7 *4	28.7	8.0 *3	5.6	7.6	6.7 *3	1.3						
5	6.5 *2	23.5	8.5 *2	2.5	4.0	7.0 *2	3.0	1.8 *2	11.7	3.7 *1	10.7	5.3 *2	13.8
6	12.0 *2	35.0	8 *1	-	4	2 *1	3	1.8 *2	4.5	3.0 *2	3.0	4.5 *2	12.0
7	5.3 *3	29.3	NO			2 *1	6	0.2 *3	11.8	0.1 *3	17.3	3.4 *3	10.1
8	2.0 *3	29.3	NO			NO		0.2 *3	13.7	1.1 *3	11.9	3.0 *4	12.1
9	2.0 *2	22.5	NO			NO		- *2	12.2	0.6 *2	9.5	1.8 *2	13.8
11	- *3	15.3	NO			- *1	6	- *3	7.5	- *3	8.8	- *2	10.3
12	- *3	14.7	- *1	-	6	- *1	3	- *3	5.6	- *3	7.8	- *4	11.1
13	- *3	14.0	- *1	-	3	- *1	-	- *3	5.6	- *3	6.3	- *3	7.3

* : number of 45-minute observation periods made during a 10-day observation period.
NO : no observations were made

Appendix 6. Example of the method used to calculate the intensity of cohesive and agonistic behavior among groups of ground squirrels for a specific 10-day period and relative to the numbers present.

PLOT 2. 1972 AGONISTIC INTERACTIONS. 10-DAY PERIOD NO. 5

	GROUPS OF SQUIRRELS INVOLVED								
	ADULT-ADULT				ADULT-YOUNG			YOUNG-YOUNG	ALL SQUIRRELS
	AA	AM	MM	AA AM MM	AY AownY	MY	AY AownY MY	YY Litt.	
A. Total number of interactions observed in this given 10-day period(from App.4B)	8	6	0	14	26	0	26	9	49
B. Average number of interactions per 45-minute period during this 10-day period (A/5)*(from App.5)	1.6	1.2	0	2.8	5.2	0	5.2	1.8	9.8
C. Average number of squirrels active per 45-minute observation period for these 10 days(from App. 5)	9.9	14.5	4.6	14.5	30.5	25.2	35.1	20.6	35.1
D. Average number of interactions per 100 squirrels per 45-minute observation period (B/C)x100 (Fig. B2 B)	16.2	8.3	0	19.3	17.0	0	14.8	8.7	27.9

* : there were five 45-minute observation periods made during the 10-day period no.5 in plot 2 in 1972

Appendix 7. Reproductive condition of adult females treated with mestranol in 1972 and 1973.

ADULT FEMALES TREATED FROM APRIL 10-12, 1972

		1972			1973
Plot #	Squirrel #	Pregnant	Lactating	Young	
2	701	?	No	No	-
"	702	?	No	No	-
"	703	?	No	No	lact,no young
"	705	Found dead April 14		-	-
"	706	?	No	No	lact,no young*
"	707	?	No	No	2 young
"	709	-	-	-	-
"	710	?	No	No	-
"	718	?	No	No	pregn.**
"	721	Yes	Yes	No	-
3	752	?	No	No	-
"	753	Yes	Yes	1 young	-
"	754	?	No	No	-
"	759	?	No	No	-
"	760	?	No	No	lact, no young
"	761	?	No	No	1 young
"	762	?	No	No	-
"	769	?	No	No	-
"	770	-	-	-	-
"	771	?	No	No	-
Other	650	-	-	-	-
"	651	?	No	No	-
"	652	-	-	-	-
"	773	?	No	No	-
"	774	?	No	No	-
"	775	-	-	-	-
"	859	-	-	-	-

ADULT FEMALES TREATED FROM APRIL 8-9, 1973

		1973			1974
2	202	?	No	No	-
"	203	Yes	No	No	-
"	226	Yes	No	No	-
"	232	Yes	No	No	-
"	234	Yes	No	No	-
"	629	Yes	No	No	?
"	718	Yes	No	No	?
"	733	?	No	No	-
"	744	?	No	No	?

? : breeding status could not be determined; Yes : is pregnant, lactating or has young when examined; No : is not pregnant, etc. ; - : squirrel no longer present; lact : lactating; pregn. : pregnant; * : treated in May 1973, no young were seen; **: retreated in April 1973, no young seen.

Appendix 8A. Average weight of adult ground squirrels trapped on plots 1, 2 and 3 during 1972.

	APRIL 1972			MAY 1972			JUNE 1972		
PLOT #	1	2	3	1	2	3	1	2	3
FEMALES									
non-treated	331 **46 (31)	303 45 (17)	293 41 (9)	386 33 (8)	324 37 (6)	297 15 (3)	570 (1)	353 66 (9)	322 33 (5)
treated*	-	252 **25 (11)	268 41 (13)	-	342 32 (8)	338 56 (6)	-	320 (1)	427 25 (3)
all females	331 **46 (31)	283 46 (28)	279 42 (22)	386 33 (8)	336 34 (14)	324 47 (9)	570 (1)	350 63 (10)	361 61 (8)
MALES									
non-treated	353 **39 (15)	313 58 (3)	330 60 (4)	399 59 (7)	395 21 (2)	350 (1)	-	460 (1)	470 70 (3)
treated	-	310 **14 (4)	327 22 (4)	-	447 25 (3)	425 78 (2)	-	530 (1)	535 21 (2)
all males	355 **39 (15)	310 34 (7)	330 42 (8)	400 59 (7)	425 35 (5)	400 70 (3)	-	495 49 (2)	495 62 (5)

( ): sample size; *: treated with a mg of mestranol in April 1972; **: standard deviation

Appendix 8B. Average weight increases of adult ground squirrels trapped repeatedly during the 1972 season. Absolute weight increases (g): Final weight minus initial weight. Relative weight increases (%) : (Absolute weight increase x 100) divided by the initial weight.

TYPES OF ADULT SQUIRRELS	WEIGHT INCREASES					
	April-May 1972			April-June 1972		
	g	%	N	g	%	N
Breeding females	38±43	12±16	13	51±49	20±20	9
Non-breeding females	98±43	40±17 ***	14	125±41	45±13 **	4
All males	89±65	28±20 *	9	-	-	-
- treated males	111±64	34±20	4	-	-	-
- non-treated males	51±37	23±17	5	-	-	-

N : sample size; *, **, *** : significantly different at 95 (*), 99 (**) and 99.9 (***) percent from breeding females when compared with chi-square tests.

Appendix 8C. Average weight of adult ground squirrels trapped on plots 1, 2 and 3 during 1973.

	APRIL 1973			MAY 1973			JUNE 1973		
PLOT #	1	2	3	1	2	3	1	2	3
FEMALES									
non-treated	331 **38 (36)	279 22 (11)	273 35 (19)	334 25 (10)	307 5 (4)	315 64 (2)	406 55 (13)	410 85 (2)	323 12 (3)
treated*	-	308 **39 (9)	-	-	332 29 (4)	-	-	-	-
all females	331 **38 (36)	292 33 (20)	273 35 (19)	334 25 (10)	320 23 (8)	315 64 (2)	406 55 (13)	410 85 (2)	323 12 (3)
MALES									
non-treated	383 **23 (3)	318 49 (5)	308 35 (7)	380 (1)	365 35 (2)	415 64 (2)	-	-	-
treated	-	292 **47 (4)	-	-	360 14 (2)	-	-	-	-
all males	383 **23 (3)	307 47 (9)	308 35 (7)	380 (1)	362 22 (4)	415 64 (2)	-	-	-

* : treated with 1 mg of mestranol in April 1973
**: standard deviation
(): sample size

Appendix 9A. Total numbers and types of cohesive interactions observed among different groups of ground squirrels on plots 1, 2 and 3 during 1972 and 1973.

TYPES OF INTERACTIONS	GROUPS OF SQUIRRELS INTERACTING																					
	PLOT 1					PLOT 2								PLOT 3								
	AA	AY	AownY	Litt	YY	AA	AM MA	MM	AY	AownY	MY	Litt	YY	AA	AM MA	MM	AY	AownY	MY	Litt	YY
1972																					
p.association*	0	6	5	11	2	1	0	1	3	24	2	8	6	0	0	0	2	5	2	0	5
nose**	1	2	2	6	1	0	2	0	5	5	1	5	3	0	1	0	0	0	0	1	5
kiss	0	0	2	0	0	0	0	0	0	1	0	3	1	0	0	0	1	0	0	0	0
grooming	2	1	16	0	0	0	1	0	1	2	1	2	1	0	0	0	0	0	1	0	0
play	0	0	2	21	7	0	0	0	0	2	0	28	3	0	0	0	0	0	1	4	2
1973																					
p.association	0	0	21	13	0	0	0	0	0	0	0	0	0	0			0	2		0	0
nose	0	1	1	5	0	0	0	0	1	2	1	0	0	0			0	1		0	0
kiss	0	0	7	14	0	1	0	1	1	2	0	0	0	0			0	2		0	0
grooming	0	0	2	4	0	0	1	1	0	0	0	3	0	0			0	0		0	0
play	0	0	2	38	0	0	0	0	0	0	0	0	0	0			0	0		0	0

*: positive association; **: all nose-to-nose, nose-to-anus or nose-to-body contacts with the exception of the kiss

Appendix 9B. Total numbers and type of agonistic interactions observed among different groups of ground squirrels on plots 1, 2 and 3 during 1972 and 1973.

	GROUPS OF SQUIRRELS INTERACTING																				
	PLOT 1					PLOT 2								PLOT 3							
TYPES OF INTERACTIONS	AA	AY	AownY	Litt	YY	AA	AM MA	MM	AY	AownY	MY	Litt	YY	AA	AM MA	MM	AY	AownY	MY	Litt	YY
1972																					
avoidance/ face-off	6	1	0	0	0	0	4	0	0	0	0	1	1	0	1	0	0	0	0	0	0
threat	3	2	0	1	3	3	1	0	1	0	0	2	2	0	0	0	0	0	0	0	1
bite		4	0						8	0	0						0	0	0		
chase/bite		4	0						2	0	0						0	0	0		
fight sec	0	2	0	4	3	0	1	0	0	0	0	0	14	0	0	0	0	0	0	0	3
chase/fight sec	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
chase	170	30	0	10	79	42	25	4	37	1	0	9	67	3	10	2	5	0	0	6	37
fight	13	6	0	10	20	15	2	0	9	0	0	6	27	6	6	4	3	0	0	2	3
chase/fight	18	6	0	2	5	11	3	0	2	0	0	7	8	0	8	4	3	0	0	0	4
1973																					
avoidance/ face-off	3	1	0	0	0	0	0	0	0	0	0	0	0	3			0	0		0	0
threat	1	6	0	15	0	2	0	1	0	0	0	0	0	4			0	0		0	0
bite		5	0						0	0	0						0	0			
chase/bite		2	0						0	0	0						0	0			
fight sec	10	1	0	14	0	1	2	1	0	0	0	0	0	10			0	0		0	0
chase/fight sec	0	0	0	5	0	0	1	0	0	0	0	0	0	2			0	0		0	0
chase	31	27	0	64	0	19	27	20	4	0	0	0	0	22			1	0		0	0
fight	11	0	0	12	0	3	1	4	0	0	0	0	0	5			0	0		0	0
chase/fight	3	1	0	9	0	2	1	3	0	0	0	0	0	3			0	0		0	0

Appendix 10. Agonistic behavior between different categories of adult females in plots 1,2 and 3 in 1972 and 1973. A. Number of agonistic interactions observed in a given 10-day period, B. Average number of adult females active per 45-minute observaton period.

10-day period	PLOT 1	PLOT 2							PLOT 3						
	AA	AA	AM	MA	MM	AA AM	MA MM	All fem.	AA	AM	MA	MM	AA AM	MA MM	All fem.
1972															
1. A	46	11	2	5	1	13	6	19	5	3	4	3	8	7	15
B	16.3	10.3	14.8	14.8	4.5	14.8	14.8	14.8	3.3	8.2	8.2	4.9	8.2	8.2	8.2
2. A	50	11	4	2	2	15	4	19	2	3	1	3	5	4	9
B	12.8	9.1	14.6	14.6	5.5	14.6	14.6	14.6	4.6	9.4	9.4	4.8	9.4	9.4	9.4
3. A	18	7	6	1	0	13	1	14	2	1	3	1	3	4	7
B	7.8	7.2	12.2	12.2	5.0	12.2	12.2	12.2	3.5	8.2	8.2	4.7	8.2	8.2	8.2
4. A	31	8	4	2	1	12	3	15	0	2	0	2	2	2	4
B	11.6	9.2	14.8	14.8	5.6	14.8	14.8	14.8	2.7	8.4	8.4	5.7	8.4	8.4	8.4
5. A	2	5	3	3	0	8	3	11	0	0	0	0	0	0	0
B	6.2	8.5	12.1	12.1	3.6	12.1	12.1	12.1	1.9	5.6	5.6	3.7	5.6	5.6	5.6
6. A	0	5	0	0	0	5	0	5	0	0	0	0	0	0	0
B	3.4	6.6	7.5	7.5	0.9	7.5	7.5	7.5	3.1	3.8	3.8	0.7	3.8	3.8	3.8
7. A	-	0	-	-	-	-	-	0	0	-	-	-	-	-	0
B	-	4.4	-	-	-	-	-	4.4	2.3	-	-	-	-	-	2.3

10-day period	PLOT 1	PLOT 2							PLOT 3						
	AA	AA	AM	MA	MM	AA AM	MA MM	All fem.	AA	AM	MA	MM	AA AM	MA MM	All fem.
1973															
0. A	20	3	0	2	5	3	7	10	14						
B	24.0	10.0	14.7	14.7	4.7	14.7	14.7	14.7	11.7						
1. A	6	0	2	1	2	2	3	5	4		No mestranol				
B	21.3	10.0	14.7	14.7	4.7	14.7	14.7	14.7	10.3						
2. A	7	4	0	0	2	4	2	6	2		treated females				
B	19.0	7.6	13.0	13.0	5.4	13.0	13.0	13.0	6.5						
3. A	14	1	1	1	5	2	6	8	4		in plot 3-1973				
B	17.3	7.7	13.2	13.2	5.5	13.2	13.2	13.2	6.8						
4. A	4	1	1	2	1	2	3	5	4						
B	6.7	6.7	11.3	11.3	4.6	11.3	11.3	11.3	5.4						
5. A	2	1	0	1	0	1	1	2	2						
B	6.5	7.5	9.0	9.0	1.5	9.0	9.0	9.0	6.3						
6. A	1	0	-	-	-	-	-	0	0						
B	12.0	6	-	-	-	-	-	6	2						
7. A	0							NO	0						
B	5.3								2						
8. A	0							NO	NO						
B	2.0														
9. A	0							NO	NO						
B	2.0														

Appendix 11. Comparison of adult agonistic behavior through Mann-Whitney tests for plots 1, 2 and 3 during the 1972 and 1973 seasons: comparison of seasonal 10-day averages for the average numbers of agonistic acts per 100 squirrels per 45-minute observation period for all adults (averages given in Table 18) and for adult females only (Table 17).

Comparison of interaction levels			PLOTS COMPARED (I vs II) AND LEVEL OF SIGNIFICANCE											
			WITHIN 1972					WITHIN 1973				1972 vs 1973		
a group of squirrels from plot I	vs	a group of squirrels from plot II	1 vs 2	1 vs 3	2 vs 3	2 vs 2	3 vs 3	1 vs 2	1 vs 3	2 vs 3	2 vs 2	1 vs 1	2 vs 2	3 vs 3
1. AA	vs	AA	*N.S.	S.97	N.S.			N.S.	N.S.	N.S.		N.S.	-	-
			**N.S.	S.95	S.95			N.S.	N.S.	N.S.		N.S.	S.95	-
2. AA	vs	MM	S.97	S.95	-	S.99	N.S.	-	-	-	N.S.			
			-	-	S.99	S.99	N.S.	N.S.		-	N.S.			
3. AA	vs	AA+AM	N.S.	S.95	-			N.S.		-				
			-	-	S.99			-		-				
4. AA	vs	AA+MM	S.97	N.S.	-	-	-	N.S.		-	-			
			-	S.95	S.99	-	-	-		-	-			
5. AA	vs	AA+MM+	N.S.	S.95	N.S.			N.S.		N.S.			-	
			N.S.	S.95	N.S.			N.S.		N.S.			-	
6. AM	vs	MA			-	N.S.	N.S.				-			
					-	N.S.	N.S.				N.S.			

Comparison of interaction levels			PLOTS COMPARED (I vs II) AND LEVEL OF SIGNIFICANCE											
			WITHIN 1972					WITHIN 1973				1972 vs 1973		
a group of squirrels from plot I	vs	a group of squirrels from plot II	1 vs 2	1 vs 3	2 vs 3	2 vs 2	3 vs 3	1 vs 2	1 vs 3	2 vs 3	2 vs 2	1 vs 1	2 vs 2	3 vs 3
7. MM	vs	MM			N.S. N.S.								– S.97	
8. AA+AM	vs	AA+AM			– S.97								– S.99	
9. AA+AM	vs	MA+MM				S.99 S.99	N.S. N.S.				N.S. N.S.		– S.99	
10. AA+AM+ MA+MM	vs	AA+AM+ MA+MM			N.S. N.S.								N.S. N.S.	
11. AM+MA	vs	AM+MA			N.S. –									
12. MA+MM	vs	MA+MM			– N.S.								– S.99	
13. AA+AM +MA+MM	vs	AA												N.S. N.S.

– : a dash means that the given comparison is possible but was not judged necessary to the discussion. Otherwise, empty space indicates that such a comparison was not possible usually because a given combination of squirrels groups did not exist in those plots.

* : first line of each group of squirrels gives results of tests for all adults

** : second line gives results for adult females only

Appendix 12. Average activity of adult resident squirrels present on plots 1, 2 and 3 during the periods of April to July 1972 and 1973.

NUMBER OF SQUIRRELS AND TREATMENT	I Number of 45-minute observation periods where this squirrel was seen between the beginning of observations and its return into hibernation *	II Total number of 45-minute observation periods made between the beginning of observations and individual returns into hibernation	ACTIVITY (I/II)x100 % (S.D.)
1972			
Plot 1			
6 A	24.3	30.0	81 (12)
Plot 2			
6 A	26.0	30.7	85 (7)
5 M	21.0	27.0	78 (9)
All squirrels	23.8	29.0	82 (8)
Plot 3			
1 A	23	29	79
6 M	17.3	22.7	76 (7)
All squirrels	18.1	23.6	77 (6)
1973			
Plot 1			
17 A	13.1	18.0	73 (16)
Plot 2			
8 A	14.2	17.6	81 (12)
7 M	15.9	17.0	93 (6)
All squirrels	15.0	17.3	87 (11)
Plot 3			
10 A	13.2	15.1	87 (17)

A : non-treated adult, M : mestranol treated adult
(S.D.) : standard deviation
* : observations started on April 21, 1972 and on April 16, 1973

Appendix 13. Resident adult home ranges and core areas: areas covering 50%, 75% and 100% of all the points (radiating from the home burrow) where squirrels were observed in plots 1, 2 and 3 during the field seasons 1972 and 1973.

SQUIRREL NO.	BREEDING STATUS	Area including a given percentage of all observed points (m^2)		
		50% (core area)	75%	95%-100% (home range)
PLOT 1 - 1972				
788	BR	200	360	780
803	BR	370	680	1050
805	BR	185	275	600
807	BR	260	470	1030
815	BR	375	540	1025
820	BR	275	325	625
847	BR	245	540	875
801	MALE	420	560	1090
814	MALE	265	570	975
825	BR	-	-	-
PLOT 2 - 1972				
713	BR	160	320	860
726	BR	290	550	1800
741	BR	100	280	540
743	BR	250	530	900
744	BR	320	520	870
746	BR	160	350	810
747	BR	260	400	570
748	BR	220	400	1030
701	M.72	250	550	1750
702	M.72	600	1140	2010
703	M.72	160	280	590
706	M.72	160	370	590
718	M.72	200	300	900
721	M.72	200	400	750
735	MALE	170	280	950
695	MALE	-	-	-
704	MALE	-	-	-
724	BR	-	-	-
749	BR	-	-	-
707	M.72	-	-	-
745	M.72	-	-	-
PLOT 3 - 1972				
752	M.72	250	420	1470
753	M.72	380	600	1880
754	M.72	320	470	1050
760	M.72	500	590	1050
761	M.72	320	490	1100
762	M.72	370	570	900
755	BR	170	610	1590
756	BR	460	610	1140
790	MALE	-	-	-
769	M.72	-	-	-

PLOT 1 - 1973				
102	BR	200	440	730
108	BR	210	340	490
111	BR	135	265	800
112	BR	210	320	690
126	BR	220	330	730
857	BR	480	1110	2060
861	BR	140	260	710
866	BR	280	400	880
874	BR	380	730	1650
889	BR	160	340	710
896	BR	100	210	350
935	BR	230	540	710
937	BR	260	680	1020
870	BR	-	-	-
PLOT 2 - 1973				
208	BR	100	180	260
211	BR	180	330	860
692	BR,M.May73	470	870	1560
693	BR,M.May73	340	910	1320
703	BR,M.72	270	530	670
706	BR,M.72 M.May73	110	170	240
202	M.73	120	250	650
214	M.73	200	380	800
226	M.73	260	560	1020
629	M.73	180	400	970
718	M.72,M.73	190	290	680
744	M.73	330	780	1350
205	MALE	310	720	1400
655	MALE,M.72	170	280	470
682	MALE	-	-	-
642	M.73	-	-	-
PLOT 3 - 1973				
310	BR	390	970	1450
761	BR,M.72	540	820	1440
413	Pregn,no young	450	1080	1940
756	Pregn,no young	190	360	1240
794	Lact,no young M.72	590	1050	2030
306	N.BR.	200	410	570
307	N.BR.	490	1010	1630
304	MALE	1060	2490	3350
301	MALE	-	-	-
302	N.BR.	-	-	-

BR : adult female observed with young
MALE :adult male non-treated with mestranol
M.72 : adult squirrel, female unless specified, treated with mestranol in April 1972
M.73 : same as above,except treated in April 1973
M.May73 :adult female treated when lactating in May 1973
Pregn : female was palpably pregnant, considered as breeding
Lact : female had swollen teats and was lactating, considered as breeding
N.BR. : females were never observed to be pregnant, lactating and were never observed with young although they were never treated with mestranol

Appendix 14. Levels of significance of Mann-Whitney ranking tests comparing the densities of active squirrels found in plots 1, 4, 5 and 6 during 1973 (period 5-13) and their levels of agonistic behavior.

	Density of a group of squirrels from plot I versus Density of a group of squirrels from plot II *		
PLOT I versus PLOT II	1. A vs A	2. A+Y vs A+Y	3. Y vs Y
1 vs 4	N.S.	S.99	S.99
1 vs 5	N.S.	S.99	S.95
1 vs 6	N.S.	N.S.	N.S.
4 vs 5	N.S.	N.S.	N.S.
4 vs 6	S.97.5	S.97.5	N.S.
5 vs 6	N.S.	N.S.	N.S.

	Level of agonistic acts of a group of squirrels from plot I versus Level of agonistic acts of a group of squirrels from plot II **		
PLOT I versus PLOT II	1. AA vs AA	2. AY vs AY	3. YY vs YY
1 vs 4	N.S.	N.S.	S.95
1 vs 5	N.S.	N.S.	S.99
1 vs 6	N.S.	S.97.5	S.99
4 vs 5	N.S.	N.S.	N.S.
4 vs 6	N.S.	S.95	N.S.
5 vs 6	N.S.	N.S.	N.S.

* : from Table 25, ** : from Table 26

Appendix 15. Levels of significance of Mann-Whitney ranking tests comparing the average numbers of agonistic interactions occurring between adults and juveniles, and among juveniles in plots 1, 2 and 3 during 1972 and 1973.

Level of agonistic acts from a group of squirrels from plot I
versus
Level of agonistic acts from a group of squirrels from plot II

PLOT I versus PLOT II	1. AY+AownY+MY vs AY+AownY+MY	2. AY vs MY	3. AY vs AY	4. MY vs MY	5. Litt+YY vs Litt+YY	6. Litt vs YY	7. Litt vs Litt	8. YY vs YY
WITHIN 1972								
1 vs 2	N.S.		N.S.		N.S.		N.S.	N.S.
1 vs 3	N.S.		N.S.		N.S.		N.S.	N.S.
2 VS 3	N.S.		N.S.	N.S.	N.S.		N.S.	N.S.
1 vs 1						S.99		
2 vs 2		S.99				S.99.9		
3 vs 3		N.S.				S.95		
WITHIN 1973								
1 vs 2	N.S.		N.S.		S.99.9		S.99	N.S.
1 vs 3	N.S.		N.S.		S.99.9		S.99.5	N.S.
2 vs 3	N.S.		N.S.		N.S.		N.S.	N.S.
1 vs 1						S.95		
2 vs 2		N.S.				N.S.		
3 vs 3						N.S.		
1972 VS 1973								
1 vs 1	N.S.				N.S.		S.95	S.95
2 vs 2	N.S.		N.S.	N.S.	S.99		N.S.	S.99.5
3 VS 3	N.S.				S.99		N.S.	S.99.5

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