INFLUENCE OF THE SOCIAL HIERARCHY ON GRAY SQUIRREL BEHAVIOR

by

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INTRODUCTION

Habitat improvement is currently the most effective tool in wildlife management. It seeks to increase game populations by providing those requirements that are present in the least quantity and are consequently limiting the population. Unfortunately, at times the limiting factors are difficult to isolate and identify. Food is normally the factor that puts an upper limit on population density (Wynne-Edwards, 1962). Animals can become so numerous as to destroy themselves by destroying their food supply, or they can develop a system which will limit their numbers before destruction of their food supply occurs. Wynne-Edwards' (1962) hypothesis that higher forms of animals can impose self-limitations on their own numbers has been growing rapidly in favor among animal ecologists. To arrive at this self-limitation of numbers, selection would favor social organizations which could impose a density-dependent control to avoid over-exploitation of available resources. The hierarchial system of social organization in animals could have evolved for this specific purpose. The social hierarchy can result in individuals being deprived of the right to breed and feed; at the ultimate level, social organization could even involve life or death (Wynne-Edwards, 1962). This investigation was initiated to obtain more knowledge of the social hierarchy and its effect on behavior of gray squirrels. Adequate social hierarchial information could lead to a more precise understanding of behavior as a density-control factor in squirrel populations.

The major objectives of this project were (1) to determine the social hierarchy of two gray squirrel populations and (2) to relate dominance of gray squirrels in a social hierarchy to sex, age, breeding behavior, and size of home range. Other considerations of this study were to determine the relationship of social dominance in squirrels with feeding activity, overwinter mortality, and shock losses. Since the social hierarchy can result in individuals being deprived of food (Wynne-Edwards, 1962), the investigation sought to determine if low ranking squirrels in the social hierarchy are forced to feed under inclement weather conditions. In addition, if social strife is an important regulating mechanism, those squirrels which were under the most social stress would likely be the ones dying of shock and disappearing from the population during the winter when stress is greatest.

LITERATURE REVIEW

Many of the early observations of squirrel behavior were only incidental to ecological and management research. Gordon (1936) noted what he thought was territorial behavior and social dominance among several members of the family Sciuridae. Hungerford and Wilder (1941) observed homing behavior of squirrels in Connecticut. Baker (1944) studied breeding behavior of squirrels. Perry (1948) noted the mating chase, season of breeding, rearing of young and movements of squirrels during his study on the breeding potential of gray squirrels.

The first research in which squirrel behavior was the primary objective did not appear until Bakken (1952) conducted studies to compare the individual behavior of fox squirrels and gray squirrels. Bakken did not attempt to determine a hierarchial organization, but he noted dominance in both fox and gray squirrels. Flyger (1955) believed that squirrels have a social organization based on seniority similar to Schein's (1954) observation of cattle. Flyger (1955) found that males were victorious over females in 75% of 64 encounters and that 80% of 59 encounters between adults and immatures (sex ignored) were won by older squirrels based on observations of one squirrel challenging another at feeders. Bakken (1959) said that social rank varied greatly with sex and age.

Although the mating chase of gray squirrels has been observed by many people, Bakken (1952) was the first to present evidence that dominance was of importance in a squirrel mating chase. He observed three chases. Based on nearness to the female, one dominant male maintained the number one position, and the other males maintained their same respective positions in all three chases. Unfortunately, Bakken did not indicate social rank of the squirrels in the three mating chases in relations to the other squirrels in the study area. The number one or dominant squirrel in the chase had the largest home range of all squirrels in the study area. Bakken did not determine a social hierarchy so he did not indicate the rank of the female in the chase or whether it was the same female each time.

Bakken noticed that young squirrels, when first emerging from the nest, had an extremely small radius of movement; he believed home range increased with age in both sexes and was larger in males in all age categories. On the other hand, Flyger (1960) could find no significant difference between the size of the home ranges of adult males, of adult females, and of immatures.

No consistent response of gray squirrel activity has been reported by writers in relation to temperature, precipitation, wind velocity, sky cover, or snow cover. Shipley (1941), Goodrum (1937), and Cross (1942) observed that low temperature, especially when accompanied by high wind, limited activity of gray squirrels more than any other weather influence. Hicks (1949) reported that wind velocity was one of the most

influential environmental factors affecting fox squirrel activity. Shipley (1941) observed that although squirrel activity was reduced during periods of low temperatures accompanied with high winds, squirrels were active under these conditions.

During trapping operations in two woodlots of the Virginia Polytechnic Institute College Farm, some squirrels are lost each year from what appears to be psychological "shock" caused by trap confinement. Trapping had to be discontinued during certain years because too many squirrels were lost from shock. Guthrie (1965) worked on shock in squirrels at Virginia Polytechnic Institute. He pointed out that although Flyger (1955) did not think social strife acted as a population regulatory mechanism, the gray squirrel could bear further study in light of its known susceptibility to confinement stress resulting in mortality.

No researcher has attempted to determine if a relationship exists between overwinter mortality and social dominance. Uhlig (1955) mentioned that juveniles generally make up the largest segment of a late fall squirrel population and therefore sustain most of the mortality. Lack (1954) wrote that in all animals the death-rate is higher in the juveniles than in the adult segment of the population. Allee (1958) believed there are many reasons for thinking that there is survival value resulting from high positions in a social hierarchy, especially in time of famine or during other periods of environmental stress. Bakken (1952) noted increased stress as indicated by social

aggressiveness in squirrels in the fall. Bakken said that this aggressiveness among gray squirrels may not appear until January if there is a good mast crop. If social strife is a density-dependent regulator, it would influence overwinter mortality during the winter period of food shortage.

TECHNIQUES AND PROCEDURES

General Information

The study was conducted on North Crumpacker Woods and Crumpacker Woods which are isolated woodlots on the Virginia Polytechnic Institute College Farm. The forest cover type of both woodlots is mature to overmature white oak-hickory. The ground cover in North Crumpacker is grass, and visibility of the entire study area is possible from a single vantage point. In contrast, at Crumpacker Woods the ground cover is composed of a dense thicket of woody shrubs and herbaceous material which restricted the field of view of the observer. North Crumpacker is 7.8 acres in area, and Crumpacker Woods is 17.9 acres.

Social Hierarchy

It was necessary to trap and mark squirrels so individuals could be visually recognized in order to determine the social hierarchy of squirrels. Two artificial feeders were used in each woodlot to congregate squirrels so more contacts would be made among individuals. Observations were made during the winter from a blind and a 20-power spotting scope was used to observe behavior and identify individuals.

Trapping

Squirrels were trapped initially for three weeks in August, 1965, in box traps described by Mosby (1955). The traps were checked twice daily to minimize shock losses caused by long confinement periods before the social hierarchies were established. Thereafter, squirrels

were trapped one week of each month until May, 1966, to gather shock loss data, to obtain overwinter mortality information, to mark new individuals, to touch-up squirrels marked with dye, and to retag squirrels that had lost tags.

Marking

Squirrels were marked by three methods. Initially, 54 squirrels were ear-marked with combinations of 5/8" disc tags. Seventeen were marked with 3/8" disc tags and 20 squirrels were dyed with varying patterns using Nyansol D, a commercial hair dye. As a means of permanent identification, all squirrels were ear-tagged with size 1 monel tags. Of the 71 squirrels marked with disc tags, 20 lost these tags and had to be dyed because their ears were mutilated and would no longer hold disc tags. Only one squirrel was known to lose the dye; however, it was retrapped and identified by its numbered monel ear tags. Hair on the terminal portion of the tail of males was clipped; females had the basal portion of the tail clipped.

Disc tags and monel tags were obtained from the National Band and Tag Company, Newport, Kentucky. The Nyanzol D dye and instructions for use were obtained from Nyanzol, Incorporated, P. O. Box 899, Lawrence, Massachusetts.

Recording of Social Hierarchial Data

The following criteria were used to determine the social dominance among gray squirrels:

1. One squirrel physically forced another off the feeder.

2. If two squirrels face one and another at the feeder but had no physical contact, the loser was the individual that left the feeder or was chased away (Fig. 1).
3. If a squirrel approached a feeding station, observed another squirrel feeding, made no attempt to challenge the squirrel at the feeder, and remained at the feeding station consuming corn dropped on the ground, it was considered a loser.
4. A chase wherein one squirrel attacked and pursued another was considered a social interaction. The squirrel being pursued was the loser.

Ranking of Squirrels

Squirrels were ranked in a social hierarchy by two methods. One method used by Komai, Craig, and Wearden (1959) in ranking chickens, was the percentile social rank formula. The rank of an individual (X) is calculated as (A+B)/2. A is the percentage of squirrels that X dominated, and B is equal to 100% minus the percentage of squirrels dominating X. To be given a percentile social rank, a squirrel had to have encountered at least five other individuals. The second method was to rank squirrels linearly where an individual is dominant over the squirrel immediately below in rank but is submissive to the squirrel above in rank. This method requires no computations and is based entirely on the observed social interactions in the field.

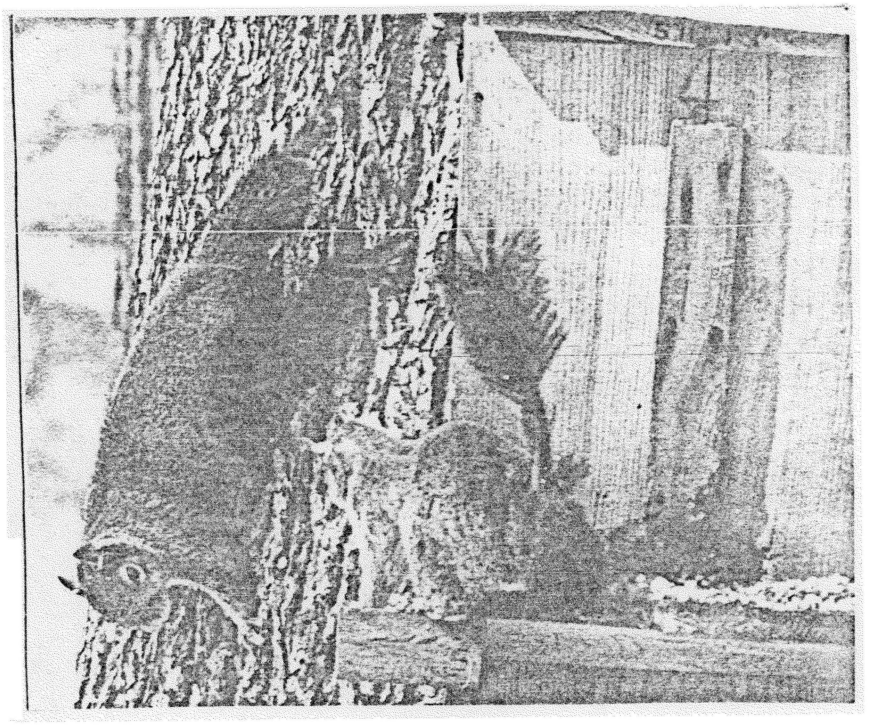

Fig. 1. Social interaction between two gray squirrels at feeder. Note monel tags on ears; squirrel on left is a male with terminal portion of tail clipped. Squirrel on right is a female with basal portion of tail clipped. Appendages are dyed on each of these squirrels.

Sex and Age

Squirrels were sexed by examination of the external genitalia. Squirrels were aged by tail pelage and by characteristics of the external genitalia as described by Sharp (1958). Squirrel trapping, tagging, and aging has been performed in the two study woodlots for 10 to 15 years. Many squirrels tagged previously could be accurately aged to year-class instead of classifying them only as juveniles, subadults, or adults. Testing the relationship of social dominance with sex was accomplished by observing whether males or females won the most social interactions.

Correlation of social rank with age was presented statistically by the Spearman rank correlation coefficient (Siegel, 1956). Using this method, the two variables (X,Y) being tested for correlation are ranked and a correlation coefficient computed. The formula used for calculating the correlation coefficient is as follows:

$$\text{Spearman rank correlation coefficient } (r_s) = \frac{\sum x^2 + \sum y^2 - \sum d^2}{2\sqrt{\sum y^2 \sum x^2}}$$

$\sum$ = Summation

$x^2 = \frac{N^3 - N}{12}$

N = Number of observations of the X variable

$y^2 = \frac{N^3 - N}{12}$

N = Number of observations of the Y variable

d^2 = Sum of squared differences in rank between individuals on X variable and Y variable

In testing correlations, the null hypothesis assumes that the two variables are not related. The alternative hypothesis is that they are related. The region of rejection of the null hypothesis consists of all values of the measure of association which are so extreme that the probability associated with their occurrence under the null hypothesis is equal to or less than the significance level for the given degrees of freedom.

Breeding Behavior

Dominance order of males in mating chases were recorded to obtain information of the role of social dominance in the right to breed. Females being chased were identified and recorded.

Home Range

Determination of home ranges was accomplished by plotting on a map where squirrels were first trapped, recaptured, and locating where squirrels were observed by a field map with reference trees indicated. Each reference tree was a trapping station and was easily identified in the field by numbers painted on the tree. The point of activity of a squirrel was not recorded more than one time per hour, and the position of the animal was plotted on the map where it was first identified that given hour.

A minimum of five points were used to measure the area of the home range for each individual. Points on a map maintained for each squirrel were connected by straight lines. The area of the resulting figure was measured by a planimeter and converted to acres.

Feeding Activity

To determine if there was an association between social rank and feeding activity in inclement weather, field records of feeding activity under varying weather conditions were maintained. The number of squirrels seen each hour was recorded each morning from 6:00 AM to 12:00 Noon because squirrels are generally most active during this period of the day (Bakken, 1952).

Wind was measured by using a modified form of the Beaufort scale as shown in Table 1.

Cloud cover was measured by a photoelectric exposure meter placed on an aluminum-painted frame (Mosby, 1963). A day with a reading less than 100 was considered as dull. Readings from 100 to 250 were rated as cloudy; a measurement over 250 was considered as clear. All readings were taken in the morning.

In North Crumpacker, the Spearman rank correlation coefficient was computed to illustrate the correlation of social rank and feeding activity in wind rated Beaufort scale 3. Each squirrel was ranked by activity through the use of an activity value equal to the number of times the squirrel was observed in number 3 wind divided by the number of months that the squirrel was known to have been marked. In addition, feeding activity under all weather conditions was recorded and examined by the Spearman rank correlation coefficient to determine any general differences in the amount of feeding activity between dominant and subordinate squirrels in the social hierarchy.

Table 1. Modified Beaufort scale used to measure wind velocity

Modified Beaufort number	Velocity (miles per hour)	How estimated
1	0-3	wind not felt against face
2	4-7	wind felt against face
3	8+	leaves and small twigs in constant motion

Overwinter Mortality

Mortality was based on the disappearance of squirrels from trapping and sight records as described by Flyger (1956). This technique is an indirect method, and a squirrel was assumed to be dead if it was not seen or trapped in a three month period.

Shock Losses

Shock losses that occurred when squirrels were confined in traps were recorded. Initially the traps were checked in mid-morning and late afternoon in an attempt to reduce shock losses until a social hierarchy was recognized. Traps were checked in the late evening to prevent overnight confinement. After the social hierarchies were established, traps were checked daily at midday.

RESULTS AND DISCUSSION

Social Hierarchy

A total of 417 hours were spent in the two study woodlots collecting the observational data reported below. One or more squirrels were under observation during all of the 417 hours except for 23 hours. A total of 43 marked squirrels were observed engaging in 638 social interactions in North Crumpacker, and 19 marked squirrels were involved in 112 social interactions in Crumpacker. Thus, the results reported below are based on 62 marked squirrels involved in 750 social interactions.

Social hierarchies were constructed in each woodlot from these social interactions. These social hierarchies, as observed in gray squirrels were "linear right" hierarchies. As used in this report, "linear right" hierarchy infers that the alpha squirrel in the social hierarchy dominates all others; beta dominates all but alpha, and so on down the line. It also infers that in all social encounters between two individuals, one squirrel is victorious over the other.

Confidence of ranking squirrels linearly in the social hierarchy could be assumed because of the low frequency of reversals in assigned rank. In the combined total of 750 expressions of social dominance, only 25 or 3% were reversals. In 16 of these reversals, the normally dominant animal reasserted his dominance in subsequent social interactions.

A total of 39 squirrels were ranked by the percentile formula and 29 by the linear method. Forty-nine to 71% of all possible unidirectional

interactions were observed among the squirrels ranked in the social hierarchy (Table 2). The correlation coefficient between the two methods of ranking was significant at the 1% level (Table 3).

The most surprising characteristics of the social hierarchy of squirrels was its rigidity. The writer could predict with precision which of two squirrels would win a social interaction. This rigidity implies a rather good memory with respect to individual recognition of other squirrels in the woodlot. Actual combat among squirrels was a rarity, and this indicates stability in the social structure. The writer only noted three fights. When combat was observed, it was very ferocious. In one fight, the two individuals involved fell from the same tree twice before the fight ended; one of the falls was approximately 30 feet.

Avoidance behavior was evident when subordinate squirrels would not attempt to challenge dominant squirrels at the feeder. Even when the subordinate squirrels were permitted free access to the feeders, they approached the feeder very cautiously and displayed anxiety by maintaining constant vigilence for other squirrels that might approach the feeder.

Sex and Age

Generally, males were dominant over females. Males were victorious over females (Table 4) in 79% of 323 interactions. Comparing equivalent age classes, the males won 66% of 128 interactions. Seven of the 10 most dominant squirrels in the social hierarchy at North Crumpacker

Table 2. Two methods of ranking gray squirrels including the number of squirrels ranked by each method and the percent of all possible unidirectional social interactions engaged by the squirrels, North Crumpacker Woods and Crumpacker Woods, V. P. I. College Farm, 1965-66

Method of ranking	North Crumpacker Woods		Crumpacker Woods	
	Number of squirrels in social hierarchy	Percentage of unidirectional interactions	Number of squirrels in social hierarchy	Percentage of unidirectional interactions
Percentile formula	30	49	9	65
Linear method	20	65	10	71

Table 3. Correlation of the percentile method of ranking gray squirrels in the social hierarchy with the linear method of ranking, North Crumpacker and Crumpacker Woods, V. P. I. College Farm, 1965-66

Study area	Number of squirrels ranked to test r_s	Spearman rank correlation coefficient (r_s)	Significance level 5%	Significance level 1%
Crumpacker	20	0.915	0.377	0.432
North Crumpacker	7	0.936	0.714	0.893

Table 4. Social interactions between male and female gray squirrels, irrespective of age, and interactions between males and females of equivalent age-classes. Equivalent age-classes used were adults challenging adults, subadults challenging subadults, and juveniles challenging juveniles. North Crumpacker Woods and Crumpacker Woods, V. P. I. College Farm, 1965-66

Sex of squirrels winning interactions	Social interactions among all age classes		Social interactions among equivalent age classes	
	Number	Percentage	Number	Percentage
Males	253	79	85	66
Females	70	21	43	34
Totals	323	100	128	100

were males. At Crumpacker, the five most dominant squirrels ranked by percentile formula, were three females and two males. By linear ranking, the five most dominant squirrels were four males and one female. Approximately one-half of the squirrels in the social hierarchies were females.

Social rank increased with age in both woodlots (Fig. 2 and 3). The correlation of social rank with age was greater (Table 5) in the social hierarchies determined by linear ranking (North Crumpacker r_s = .631 and Crumpacker r_s = .789).

The writer thinks that the increase of rank with age is a result of several factors. Probably experience with age was very important in determining social rank. Hormonal development and size of animal might be very important also. It was noted by the writer that juvenile squirrels did not display social aggressiveness with such severity as was seen in older animals. When a juvenile squirrel approached another juvenile at the feeder, many times both squirrels would run from each other. The only incidences that more than one squirrel occupied the feeder at the same time were when two juveniles would both feed or when one particular female parent of two juveniles permitted the juveniles to share food with her at the feeder.

The writer did not examine the importance of body size, which is associated with age to a certain degree, had on social dominance of squirrels. It is possible that a correlation of size and social rank may exist. Two squirrels in particular were noted as being larger than

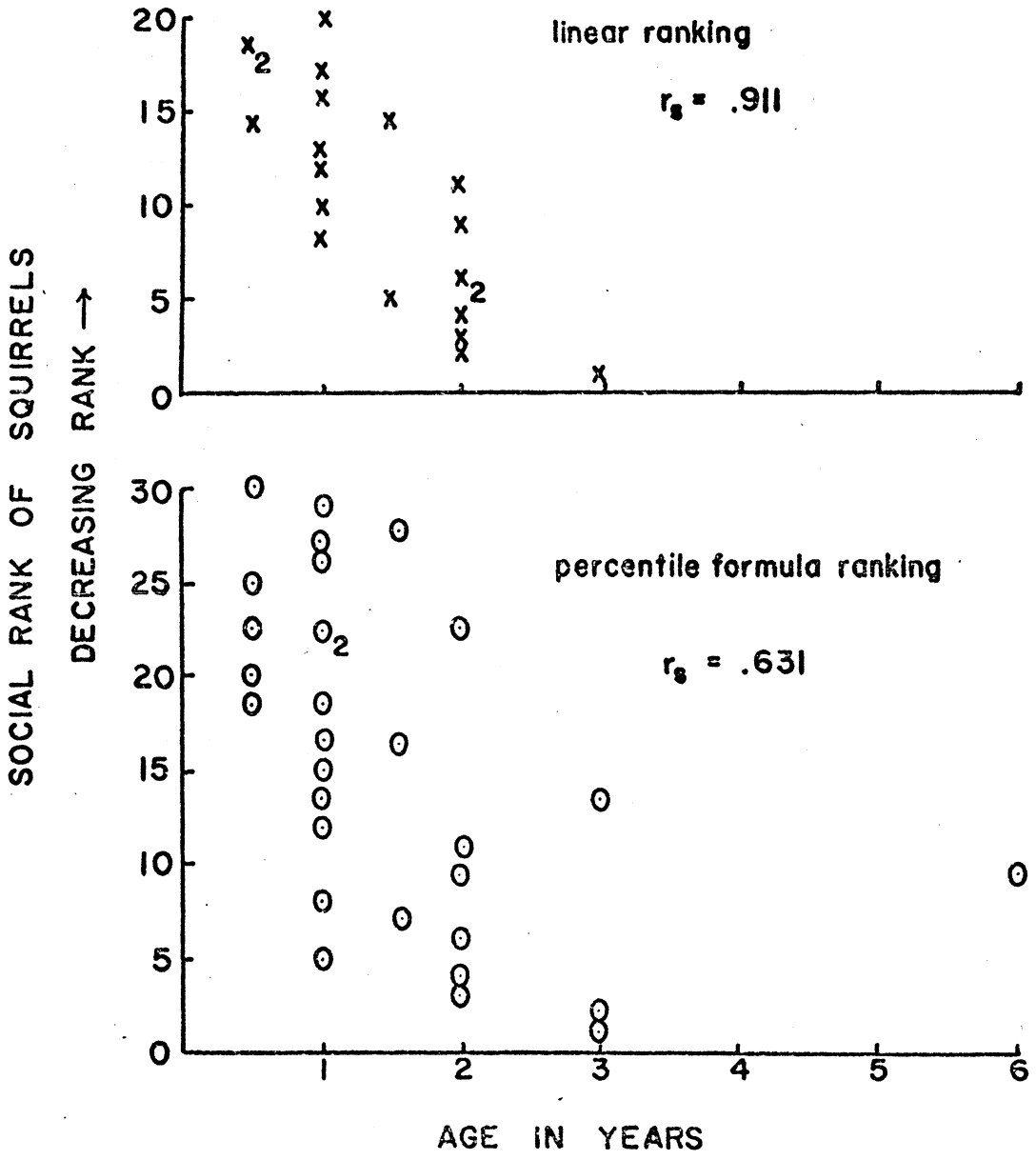

Fig. 2. Influence of age on social rank of gray squirrels at North Crumpacker Woods, V. P. I. College Farm, 1965-66; rank determined by linear ranking and by the percentile formula.

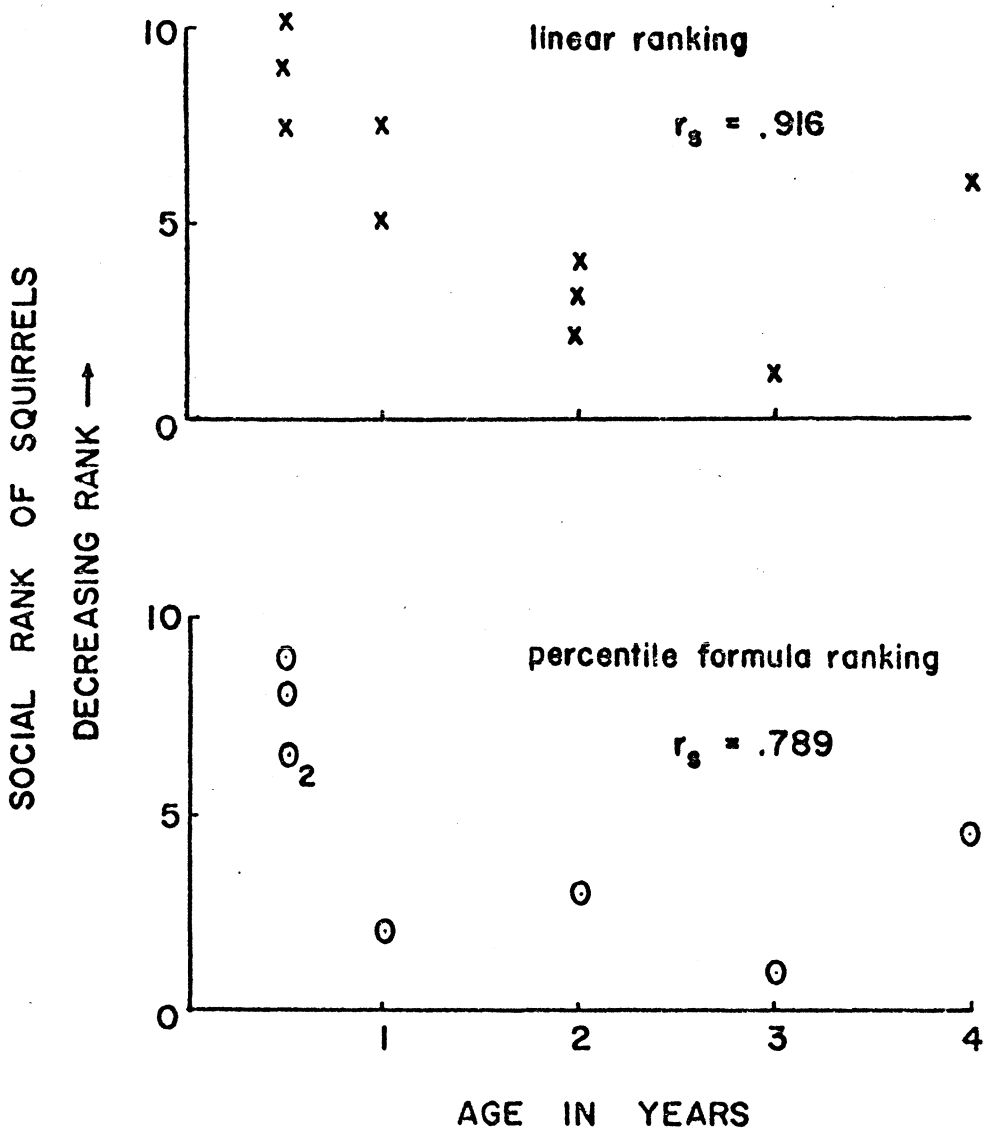

Fig. 3. Influence of age on social rank of gray squirrels at Crumpacker Woods, V. P. I. College Farm 1965-66; rank determined by linear ranking and by the percentile formula.

Table 5. Correlation of social rank and age of gray squirrels ranked by the percentile formula and by the linear ranking method, North Crumpacker Woods and Crumpacker Woods, V. P. I. College Farm, 1965-66

Method of ranking	Number of squirrels in social hierarchy	Spearman rank correlation coefficient (r_s)	Significance level	
			5%	1%
North Crumpacker				
Percentile	30	0.631	0.306	0.432
Linear	20	0.911	0.377	0.534
Crumpacker				
Percentile	9	0.789	0.600	0.783
Linear	10	0.916	0.564	0.746

other squirrels. One of these individuals was a male, and he ranked #2 in a social hierarchy of 10 squirrels at Crumpacker Woods; the other large squirrel was a female in North Crumpacker Woods which ranked #9 of 20 squirrels in the social hierarchy. This rank of #9 was the third highest position held by a female in the social hierarchy.

Breeding Behavior

By mid-December mating activity became noticeable; males followed females constantly. Usually a male would cautiously approach a female and attempt to sniff her anal region. Generally, the female moved a few feet away when the male attempted this action. The procedure would be repeated innumerable times. Sexual contacts, including the above behavior and mating chases involving several squirrels, were observed a total of 35 times - 28 times in North Crumpacker and 7 times in Crumpacker Woods. In North Crumpacker, the #1 and #2 males (percentile rank) were responsible for 37% of all sexual contacts. Marsden and Holler (1965) found that the two most dominant male cottontail rabbits accounted for 70% of all observed sexual contacts. The 4 most dominant male squirrels of the 18 males in the social hierarchy at North Crumpacker accounted for 65% of the sexual contacts. In Crumpacker, the #1 and #3 ranked males were involved in five of the seven incidences that the female following behavior was observed.

Four times the response of a male following a female developed in the familiar mating chase with more than two males chasing the same female. Three of these chases were observed in North Crumpacker Woods.

In the first chase, the #2, #5, and #12 ranked males, two unmarked squirrels, and the #16 ranked female were involved. In the second chase, the #1, #2, #4, #6, #7, #22, and an unmarked male participated; the female was not ranked. In the third chase, the males ranked #1, #3, #5, #6, and two unmarked males chased a female ranked #11 in the hierarchy. The mating chase seen in Crumpacker involved the #1 and #2 ranked male squirrels in this woodlot, two unmarked males, and a female ranked #7 out of 9 squirrels in the hierarchy.

In all chases, dominance was displayed; the most dominant male would chase the other males from the female when she stopped. This action is in contrast to rats where Etkin (1964) reports that the males do not prevent other males access to the estrus female.

Copulation was observed only three times. The males ranked #1, #2, and #22 in North Crumpacker were seen engaged in copulation.

In 21 sexual contacts, where the male nearest the female and the female involved were identified, the male ranked higher in the social hierarchy than the female. Even though observations of actual copulation were not noted in all sexual contacts, the writer thinks that mating priority, and advantage of high-ranked individuals in the social organization, was illustrated. The dominant male squirrels probably leave more progeny, and presumably those progeny would have a better chance of success.

Home Range

In North Crumpacker, the average home range of squirrels ranked by the percentile formula was 1.24 acres. Squirrels ranked linearly in the social hierarchy had an average home range of 1.45 acres.

The computed correlation coefficient of social rank and size of home range of squirrels ranked by the percentile formula was not significant at the 1% level; the correlation coefficient of rank and size of home range of squirrels ranked by the linear method was slightly significant at the 1% level (Table 6).

When the project was first initiated, the writer assumed that a high correlation might exist between social rank and size of home range. It has been shown that gray squirrels cache food at random, and the food stored by one individual may be utilized by another (Sharp, 1959). It would seem that the larger the home range of a squirrel the more likelihood of his finding more of the cached food. Therefore, if size of home range increased with social dominance, it would seem that the survival value of high positions in a social hierarchy would occur as a result of a larger food supply.

It appeared from field observations that the six most socially dominant squirrels moved freely over the major portion of the wooded area in North Crumpacker. These six squirrels appeared frequently at both feeders which were 6.5 chains apart. Only 4 other squirrels in the social hierarchy of 30 were seen at both feeders.

Table 6. Correlation of social rank and size of home range of gray squirrels ranked by the percentile formula and by the linear ranking method, North Crumpacker Woods, V. P. I. College Farm, 1965-66

Method of ranking	Number of squirrels in social hierarchy	Spearman rank correlation coefficient (r_s)	Significance level	
			5%	1%
Percentile	30	0.431	0.306	0.432
Linear	20	0.560	0.377	0.534

However, as presented above and in Fig. 4, relationship of social rank and size of home range was not as apparent as was expected. If a higher correlation between social rank and size of home range does exist than the data here indicates, the lack of correlation may be due to inherent weaknesses in the technique used to determine size of home ranges. Flyger (1960) pointed out that the size of home range of squirrels normally increases with the number of records. For example, in this study home range calculations were made only for those individuals for which 5 or more records were secured. However, according to Flyger's statement, an individual with 10 to 15 records would likely have a greater home range than would those squirrels for which only 5 observations were recorded.

Feeding Activity

Temperature and cloud cover had no significant effect on squirrel feeding activity in North Crumpacker (Table 7). Feeding activity in Crumpacker was not analyzed because not enough information was collected. The importance of rain and its influence on squirrel activity could not be accurately assessed because the writer spent only nine hours in the rain observing behavior.

Activity based on the average number of squirrels seen per hour was higher during the period when the ground was covered with snow than the average for any other environmental condition measured. The writer thinks the reason for this observation is that when the ground was covered with more than two inches of snow, squirrel usage

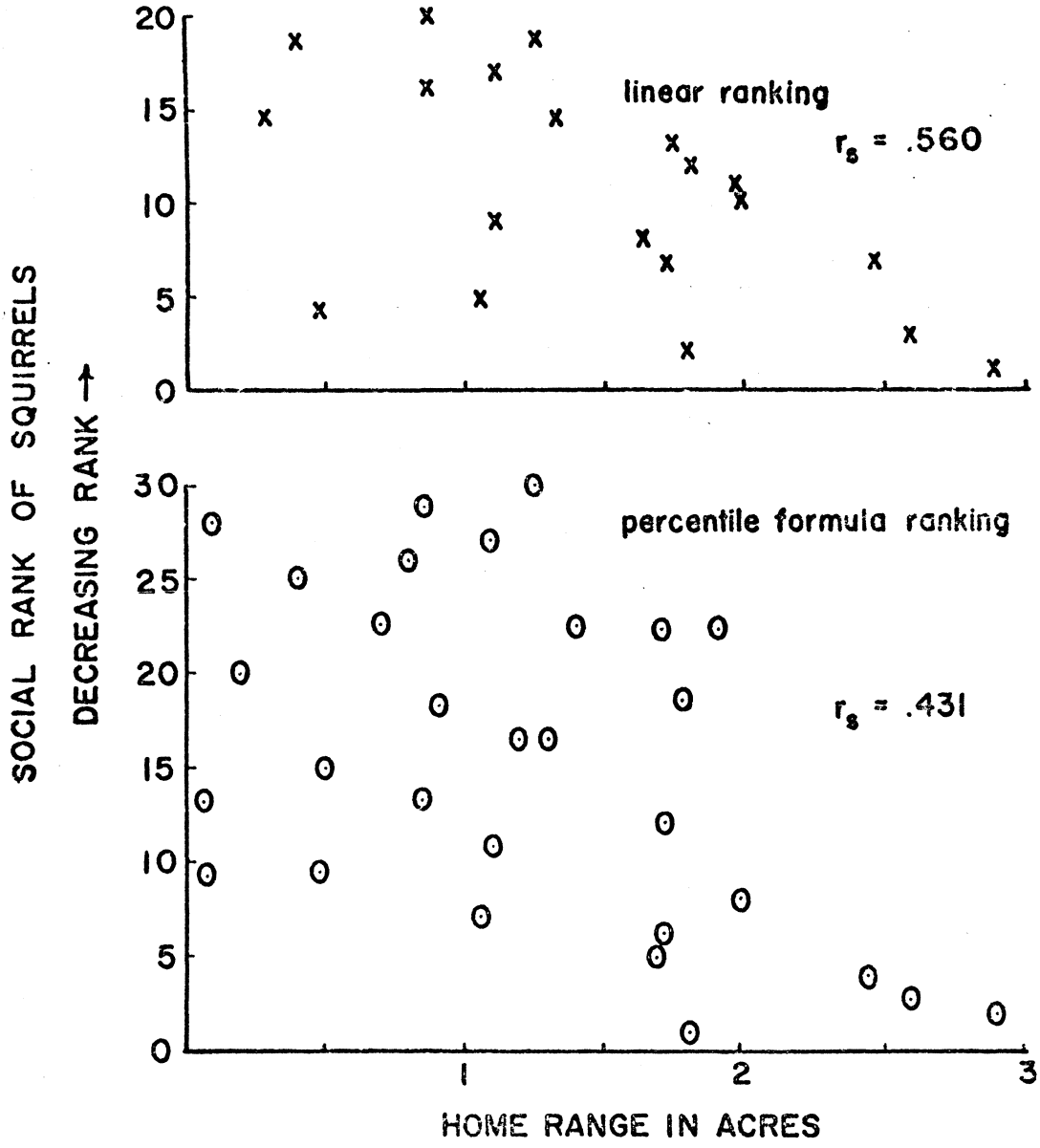

Fig. 4. Effect of social rank on the size of home ranges of gray squirrels at North Crumpacker Woods, V. P. I. College Farm, 1965-66. Social rank of squirrels determined by linear ranking and by using the percentile formula.

Table 7. Influence of weather upon activity of gray squirrels in North Crumpacker Woods, V. P. I. College Farm, 1965-66

Environmental influence	Sample (hours)	Average number squirrels seen per hour	Standard deviation
Light			
Clear	32	8.594	±2.305
Cloudy	45	7.696	±3.378
Dull	35	6.200	±5.605
Precipitation			
Raining	9	3.750	±1.936
Snowing & snow cover	19	9.263	±5.914
Wind			
Beaufort scale 1	85	8.400	±3.215
Beaufort scale 2	63	7.571	±3.392
Beaufort scale 3	35	3.857	±3.219
Temperature (^{o}F)			
14-33	56	8.482	±3.205
33-50	83	6.916	±3.335
50-83	51	5.922	±2.784

increased at the feeders. When snow was more than a foot in depth, the feeders were the only readily available source of food. If food had not been provided at the feeders, the writer doubts if the squirrels would have been as active. Hicks (1949) observed a decrease in activity of fox squirrels in snow over two inches in depth. This is probably true in gray squirrels also. Based on observations over a 13-day period when the ground was completely covered with snow in excess of two inches, only 1.5 squirrels were seen per hour at points other than at the feeder. In the 13-day period preceding the snow, 3.3 squirrels were seen per hour at points other than at the feeders.

Wind was the most important or noticeable environmental influence adversely affecting squirrel feeding activity (Table 7). On the average, more than seven squirrels were seen per hour in wind rated Beaufort scale 1 and 2. Of the 148 hours when wind was rated Beaufort scale 1 and 2, three or more squirrels were seen except during 7 hours (5%) of observation. On the other hand, three squirrels or less were seen in 19 (54%) of the 35 hours where the wind was rated Beaufort scale 3.

The Spearman rank coefficient for social rank and feeding activity was not significant at 5% level and this illustrates that social dominance had no effect on activity as a whole (Table 8). Data presented in Table 9 and Fig. 5 indicate that low ranking squirrels are not more active than dominant squirrels during high wind conditions (wind rated Beaufort scale 3). Therefore, one may conclude

Table 8. Correlation of social rank with feeding activity of gray squirrels. Social rank of squirrels were determined by the percentile formula and by linear ranking. Activity was expressed by means of an activity value equal to the number of hours that a squirrel was observed divided by the number of months that the squirrel was marked, North Crumpacker Woods, V. P. I. College Farm, 1965-66

Method of ranking	Number of squirrels in social hierarchy	Spearman rank correlation coefficient (r_s)	Significance level	
			5%	1%
Percentile	30	0.292	0.306	0.432
Linear	20	-0.039	0.377	0.534

Table 9. Correlation of social rank in gray squirrels with feeding activity in wind rated Beaufort scale 3. Social ranking was performed by using the percentile formula and the linear ranking method. Activity for each individual was expressed by an activity value equal to the number of times that a squirrel was observed divided by the number of months that it was marked. North Crumpacker Woods, V. P. I. College Farm, 1965-66

Method of ranking	Number of squirrels in social hierarchy	Spearman rank correlation coefficient (r_s)	Significance level	
			5%	1%
Percentile	30	0.386	0.306	0.432
Linear	20	0.377	0.377	0.534

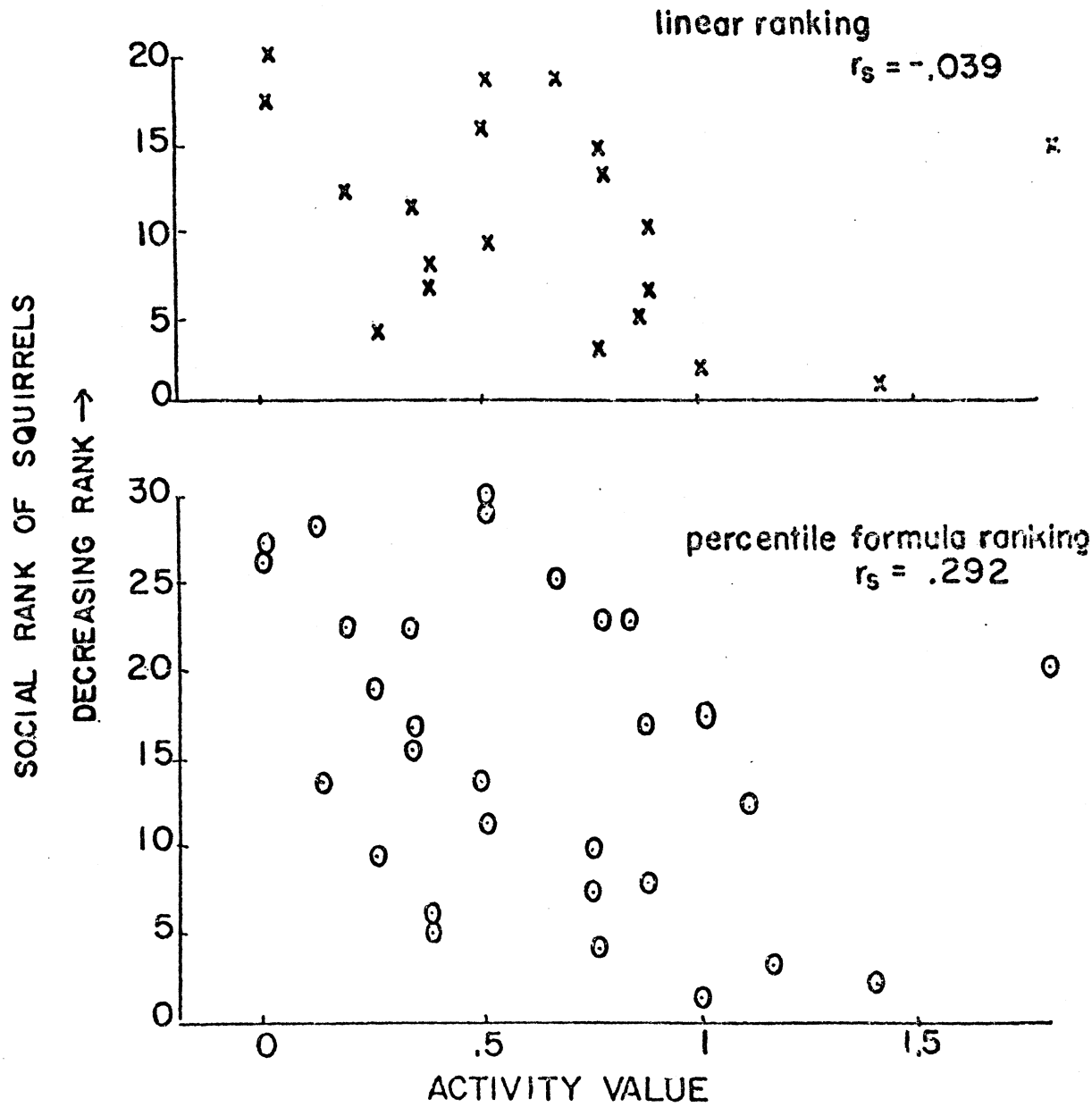

Fig. 5. Effect of social rank on feeding activity of gray squirrels in wind rated Beaufort Scale 3. Linear ranking and the percentile formula was used to determine the social rank of individuals. Activity of an individual was measured by an activity value which was equal to the number of hours the squirrel was observed in wind rated Beaufort scale 3 divided by the number of months that the squirrel was marked. North Crumpacker Woods, V. P. I. College Farm, 1965-66.

that subordinate squirrels were not forced to feed under inclement weather conditions. Perhaps it was unnecessary for subordinate squirrels to feed under inclement weather conditions more than dominant individuals because the writer did not notice any time that subordinate squirrels were denied access to food except at the artificial feeders. In areas of concentrated food supply, the subordinate squirrels may be refused access to food, but the writer did not see evidence of this.

Overwinter Mortality

Adequate data were not obtained to permit the determination of the relationship of social rank and overwinter mortality. Of the 39 squirrels considered as overwinter mortality losses, only 4 were ranked in a social hierarchy. Thirteen squirrels disappeared after the first month of trapping and were never seen again. The actual causes of mortality were not known except for those which died in traps. The lack of food should not have been a major reason for overwinter mortality because four feeders were maintained throughout the study.

Based on the conclusion that rank is correlated with age, a relationship of overwinter mortality with rank could be determined if mortality was prominent in one age class. At North Crumpacker Woods, mortality was greatest among the juveniles (Table 10). In contrast, in Crumpacker Woods mortality was greatest in the adult age class (Table 11). When mortality from both woodlots were

Table 10. Overwinter mortality of gray squirrels by age-classes at North Crumpacker Woods, V. P. I. College Farm, 1965-66

Age class	Number of squirrels marked	Including trap losses		Excluding trap losses	
		Number dead	Percentage dead	Number dead	Percentage dead
Juveniles	10	7	70	5	50
Subadults	19	5	27	3	16
Adults	25	12	48	7	28
Totals	54	24	44	12	31

Table 11. Overwinter mortality of gray squirrels by age-classes at Crumpacker Woods, V. P. I. College Farm, 1965-66

Age class	Number of squirrels marked	Including trap losses		Excluding trap losses	
		Number dead	Percentage dead	Number dead	Percentage dead
Juveniles	16	4	25	2	12
Subadults	5	1	20	1	6
Adults	18	10	55	9	50
Totals	39	15	38	12	31

combined, losses were greatest in the adult class, then juveniles; subadults had the lowest mortality (Table 12). However, as might be expected, mortality was not confined largely to any one age class. Therefore, due to inadequate data, social strife could not be proven to be a population regulator due to its influence on overwinter mortality.

Shock Losses

Data were insufficient to permit definite conclusions regarding shock mortality and social rank.

Thirteen squirrels were found dead in traps or died after being removed from traps. Two of these squirrels displayed brain damage probably caused by striking the head against the rear of a trap. Five squirrels were found dead in traps; no definite conclusions could be made as to the cause of death. Six squirrels were believed to have died of shock. None of these 13 squirrels were ranked in a social hierarchy because they succumbed before the hierarchies were established. The shock losses occurred even though the traps were initially tended twice per day and checked late in the evening to prevent overnight confinement. Oddly enough, no shock losses occurred in the spring when the traps were checked only once daily at midday. It is interesting to note, however, that 6 of the 11 squirrels which died of shock, or died in the trap, were involved in 13 social hierarchial interactions and lost every encounter. Four of the 6 squirrels had lost interactions with squirrels of known rank

Table 12. Combined overwinter mortality of squirrels at North Crumpacker Woods and Crumpacker Woods, V. P. I. College Farm, 1965-66

Age class	Number of squirrels marked	Including trap losses		Excluding trap losses	
		Number dead	Percentage dead	Number dead	Percentage dead
Juveniles	26	11	43	7	27
Subadults	24	6	25	4	17
Adults	43	22	51	16	37
Totals	93	39	42	31	33

in a social hierarchy of 30, and 2 had lost interactions with 2 squirrels of known rank in a hierarchy of 9. Four of the above six squirrels had lost interactions to low ranking squirrels; this indicates that these four squirrels probably held low positions in the social hierarchy (Table 13). The remaining two squirrels lost interactions with two high ranking squirrels, but this does not indicate whether the losers were ranked just below the dominant squirrels or at the bottom of the social hierarchy.

Table 13. Social rank of those gray squirrels which were dominant over six individuals which died presumably from shock, North Crumpacker Woods and Crumpacker Woods, V. P. I. College Farm, 1965-66

Trapping losses (X)	Number squirrels victorious over X	Lowest social rank of squirrel victorious over X	Number of social interactions won by victorious squirrels
93*	1	22 of 30	1
207	3	28 of 30	5
209	3	28 of 30	4
97	1	4 of 30	1
249	1	7 of 9	1
229	1	2 of 9	1

* Tag number

SUMMARY

Gray squirrels have a "linear right" type of social hierarchy. In social interactions between any two individuals, one individual was victorious and the other retreated. Three percent reversals were observed in 750 social interactions.

Generally males were more dominant than females, and the higher ranking positions in the social hierarchy were occupied by males. In 323 social interactions between males and females, the males won 79% of the interactions. Comparing equivalent age-classes, males won 66% of 128 social interactions.

Dominant males were responsible for most of the sexual contacts with females. The four most dominant of 18 males in a social hierarchy of 30 individuals accounted for 65% of the sexual contacts in one woodlot. In 21 sexual contacts where males and females were identifiable, the male nearest the female occupied a higher position in the social hierarchy.

There was a slight association of social rank with size of home range.

Wind was the most important environmental influence restricting squirrel feeding activity. Subordinate squirrels were not more active than dominant squirrels during inclement wind conditions.

Inadequate information was collected to determine if a relationship existed between social rank and overwinter mortality.

Adequate data were not obtained to test the relationship of social rank and its effect on shock mortality. Only 6 of 11 squirrels believed to have died from shock were involved in social interactions; however, these 6 shock-loss individuals lost all 13 interactions. Four of the six squirrels had lost social interactions to low ranking squirrels; therefore, these four squirrels probably held low positions in the social hierarchy. The remaining two squirrels lost social interactions with two high ranking individuals, but this did not indicate that the losers were low ranking squirrels.

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Appendix Table I. Data used to compute the social rank by the percentile formula* for 30 gray squirrels, North Crumpacker Woods, V. P. I. College Farm, 1965-66

Individual (X) Social rank	Tag number	Number squirrels X victorious over	Number squirrels victorious over X	Sex of X	Age of X (years)
1	5624	23	2	M	3
2	255	20	0	M	3
3	262	19	2	M	2
4	71	17	4	M	2
5	607	16	6	M	1
6	108	14	4	M	2
7	136	13	3	F	1.5
8	326	13	6	M	1
9	11	7	1	F	2
10	5069	8	2	F	6
11	620	6	5	F	2
12	79	6	6	M	1
13	5638	7	8	F	3
14	23	5	6	M	1
15	35	4	5	F	1
16	141	6	9	F	1.5
17	370	6	9	M	1
18	17	1	5	M	1
19	1	1	5	M	0.5
20	345	3	8	M	0.5
21	386	6	13	F	1
22	360	3	10	M	1
23	364	4	12	M	0.5
24	190	8	15	M	2
25	224	1	9	F	0.5
26	264	1	10	M	1
27	41	1	11	F	1
28	617	1	12	F	1.5
29	75	3	17	M	1
30	42	1	18	F	0.5

*Percentile social rank of individual (X) = A + B/2
A = percentage of squirrels "X" dominates
B = 100% minus the percentage of squirrels dominating "X"

Appendix Table II. Data used to compute the social rank by the percentile formula* for 9 gray squirrels, Crumpacker Woods, V. P. I. College Farm, 1965-66

Individual (X) Social rank	Tag number	Number squirrels X victorious over	Number squirrels victorious over X	Sex of X	Age of X (years)
1	247	6	0	M	3
2	329	7	2	F	1
3	87	5	1	M	2
4	257	3	3	F	1
5	253	3	3	F	4
6	622	2	3	M	0.5
7	234	4	5	F	0.5
8	351	2	5	F	0.5
9	393	1	5	F	0.5

*Percentile social rank of individual (X) = A + B/2
A = percentage of squirrels "X" dominates
B = 100% minus the percentage of squirrels dominating "X"

Appendix Table III. Social hierarchy of 20 gray squirrels ranked by the linear method, North Crumpacker Woods, V. P. I. College Farm, 1965-66

Individual (X)	Individuals "X" victorious over																		
255*	5624	262	--	136	71	108	607	620	---	190	386	---	141	---	75	41	43	224	---
5624		262	--	136	71	108	607	620	326	190	386	360	141	345	75	--	43	224	264
262			11	136	71	108	607	620	---	190	386	360	141	---	75	41	43	224	264
11				136	--	---	---	---	---	190	386	---	141	---	75	41	43	---	---
136					71	---	607	620	---	190	386	---	141	---	75	41	43	---	264
71							607	---	326	190	386	360	141	345	75	41	43	224	264
108							607	620	---	190	386	360	141	---	75	--	--	---	264
607								620	326	190	386	360	---	---	--	--	43	---	---
620									326	---	386	360	---	---	--	--	43	---	---
326										190	386	360	141	345	75	41	43	---	264
190											386	---	141	---	75	41	43	---	---
386												360	---	345	75	--	--	224	264
360													141	345	75	--	--	---	---
141															75	41	43	---	---
345															75	--	--	224	---
75																41	43	---	---
41																	43	---	---
43																			264
224																			264
264																			

* Tag number

Appendix Table IV. Social hierarchy of 10 gray squirrels ranked by the linear method, Crumpacker Woods, V. P. I. College Farm, 1965-66

Individual (X)	Sex of X	Age of X (years)	Individuals "X" victorious over								
247*	M	3	87	---	---	329	253	---	---	393	351
87	M	2		335	---	329	253	257	234	393	351
335	M	2			348	---	---	---	234	---	---
348	M	2				329	---	257	234	393	---
329	F	1					253	257	234	393	351
253	F	4						257	234	393	351
257	F	1								393	351
234	F	0.5								393	351
393	F	0.5									351
351	M	0.5									

* Tag number

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ABSTRACT

Based on 750 social interactions, largely at feeding stations, gray squirrels in two woodlots were ranked in a social hierarchy by the percentile rank formula and by the linear method. Correlations of rank in the social hierarchy with age, size of home range, and feeding activity under inclement wind conditions were tested statistically by the Spearman rank correlation coefficient.

The social hierarchy of gray squirrels is a "linear right" hierarchy. Males were more dominant than females, and social rank was higher with greater age. The dominant male squirrels were responsible for the majority of the observed sexual contacts with females. Size of home range increased slightly with social rank. Wind was the most important environmental factor restricting feeding activity. Subordinate squirrels in the social hierarchy were not more active than dominant squirrels during inclement wind conditions. Insufficient data were collected to determine a definite relationship of social rank with overwinter mortality and shock losses.