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REPRODUCTIVE LEVELS IN UNEXPLOITED WOODLOT FOX SQUIRRELS

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ABSTRACT

Detailed reproductive information was obtained for 138 individually-marked, female fox squirrels during 1968-1976. The population was characterized by abnormally low reproductive parameters. Production of young was 28, 11, and 0 percent among adult, subadult and juvenile cohorts, respectively. The average size of 30 litters prior to weaning was just under two. Young breeders were rare; 16 females produced their first litter at approximately 2 years of age. Only 2 of 87 adult females successfully reared two litters in a given year. Data suggest lowered reproductive levels to accommodate adverse environmental conditions.

INTRODUCTION

A long term ecological study of an urban fox squirrel (Sciurus niger rufiventer) population was initiated Fall, 1968 in Thompson Woods, a 17-acre woodlot on the campus of Southern Illinois University at Carbondale. This is believed to be the first intensively studied population of this type (Eveland 1974). This paper presents data collected December, 1968

through August, 1976 for the female segment of the population. It is concerned with reproductive performance and provides baseline information on yearly and seasonal variation in breeding rates in a population not influenced by hunter harvest. These findings will be of value in better understanding the impact of exploitation.

MATERIALS AND METHODS

Squirrels were available for examination through live-capture in box traps modified after Baumgartner (1940). Each animal was fitted with monel number 3 (National Band and Tag Co., Newport, Kentucky) and attached symbol-coded, colored vinyl ear tags. Toe clipping to the first joint provided a method for permanent identification. Quarterly (1968 to mid-1974) and weekly (mid-1974 to 1976) trapping periods provided a continuous record for the woodlot population. At each capture individual females were weighed, examined for evidence of external parasites and disease, checked for identifying tags or marks, and examined for signs of reproductive activity. If the external genitalia showed signs of estrous, a vaginal smear was taken. Upon completion of an examination each animal was released at the point of capture. Intensive field observation of marked animals and known den locations provided supplementary information as to timing of reproduction, numbers of young, and confirmed data from examinations of trapped females.

RESULTS AND DISCUSSION

During 8 years 138 females were live-trapped and marked; most contributed some information regarding reproductive levels in the Thompson Woods population. Transient animals or those suffering fatalities seldom provided enough data to evaluate reproductive performance. Only individuals repeatedly observed and captured for which a reasonably complete record

was available were included in calculations. Because reproductively active individuals are somewhat restricted in their movements while suckling young, can be confirmed through observation of dens, and can be associated with recently emerged litters, the percentages reported are considered slightly high in regards to the true proportions of all confirmed females producing young.

A total of 295 individual female breeding seasons was evaluated; of these only 67 (22.7 percent) produced offspring. Adults were productive at substantially higher levels than either subadults or juveniles (Table 1). In Oklahoma 55.6 percent of 178 adult female fox squirrels were lactating compared to 3.8 percent for subadults and 0.0 percent for juveniles (Chesemore 1975); this pattern was also apparent in gray squirrels. In Ohio Nixon and McClain (1975, p.433) found 2.2 percent (3 of 136) of 5 to 9 month old female gray squirrels to show annual breeding over a 4-year period compared to 55.8 percent for 104 (10-14 months old), and 95.4 percent of 130 adults.

Table 1. Frequency of breeding by age-class for female fox squirrels, Thompson Woods, Southern Illinois University, spring, 1969 to spring, 1976.

Breeding Age	Breeding Season	Number of Seasons	Sample Size	Number Breeding	Percent Breeding
Adult (>14 months)	Spring	8	129	50	38.8
	Summer	7	93	12	12.9
	Combined	15	222	62	27.9
Subadult (9-14 months)	Spring	8	34	4	11.8
	Summer	4	10	1	10.0
	Combined	12	44	5	11.4
Juvenile (<9 months)	Spring	4	14	0	0.0
	Summer	6	15	0	0.0
	Combined	10	29	0	0.0

Individuals of ages greater than 24 months generally bred at a higher rate than younger squirrels (Table 2). There was no evidence of a senescent effect in the age range studied with the only female exceeding 6 years of age producing a litter. The average age at first conception for 16 females marked as juveniles was approximately 24 months. Eveland (1974, p. 60) mentioned the old age of first lactation for the Thompson Woods population from data on animals first captured as adults. In contrast Brown and Yeager (1945) and Allen (1943) reported females first breeding at ages of 10 or 11 months. In only 2 of 59 instances did known-aged animals in Thompson Woods breed prior to 12 months of age.

Considering all age classes, 30.5 percent (54 of 177) of the females examined produced spring litters compared to 11.0 percent (13 of 118) which showed summer production. This difference was significant ($X_1^2 = 15.32$, $p < 0.01$) and was even more pronounced when only full adults were considered (Table 1). The seasonal performance (Figure 1) shows the most common breeding pattern to be good spring litter production followed by near or complete quiescence during summer. Only in 1975 was this not the pattern. Presumably summer production in 1975 was in response to an abundant supply of spring foods coupled with inactivity the previous breeding season. Observations and trapping through late summer and fall 1969 yielded one litter of two for the only reproductive female (an adult) in the population. Neither Brown and Yeager (1945) nor Allen (1943) mentioned such disparity between spring and summer production. Nixon and McClain (1975, p. 434) found that the gray squirrel in Ohio, showed nearly equal proportions of adult females breeding in spring and summer. Their data suggest, however that severe fluctuations in proportions of females breeding do occur.

Table 2. Production by year class by season for female fox squirrels, Thompson Woods, Southern Illinois University.

Age[a] at Breeding	Spring Season		Summer Season		Seasons Combined	
	No. Examined	No. Breeding	No. Examined	No. Breeding	No. Examined	No. Breeding[b]
less than 1 year	48	4 (8.3%)	25	1 (4.0%)	73	5 (6.8%)
1-2 years	59	14 (23.7%)	35	2 (5.7%)	94	16 (17.0%)
2-3 years	35	20 (57.1%)	30	3 (10.0%)	65	23 (35.4%)
3-4 years	20	11 (55.0%)	19	3 (15.8%)	39	14 (35.9%)
4-5 years	10	2 (20.0%)	5	1 (20.0%)	15	3 (20.0%)
5-6 years	5	3 (60.0%)	3	2 (66.7%)	8	5 (62.5%)
6-7 years	0	-	1	1 (100.0%)	1	1 (100.0%)
Totals	177	54 (30.5%)[c]	118	13 (11.0%)	295	67 (22.7%)

[a]Animals captured as adults placed in categories according to minimum known ages.

[b]Significant difference in proportions breeding for age classes, $X^2_6 = 32.69$, $p<0.01$.

[c]Significant difference in proportions breeding in spring versus summer, $X^2_1 = 15.32$, $p<0.01$.

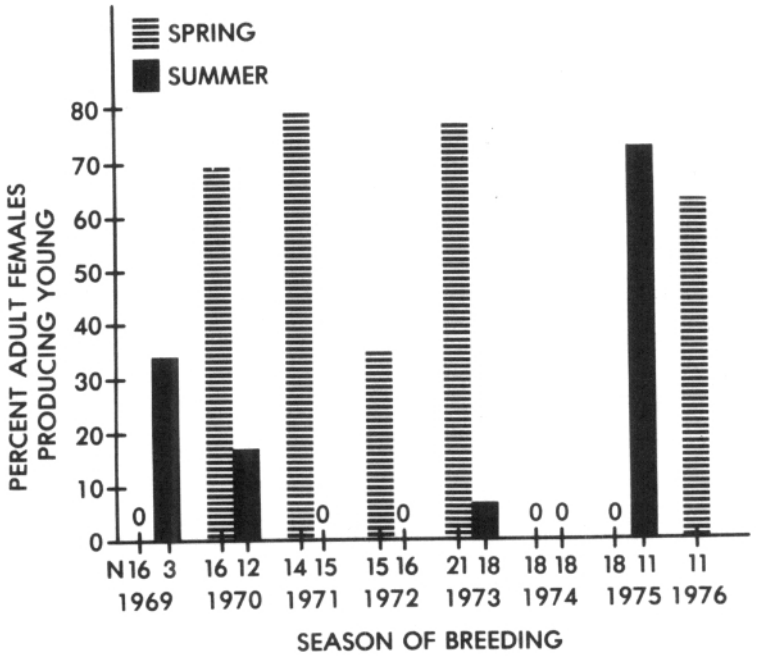

Figure 1. Reproductive performance by season of breeding for adult female fox squirrels, Thompson Woods, 1969-76.

Chesemore (1975, p. 270) showed a relatively high percentage of females lactating during both seasons in Oklahoma.

Of 87 females examined both spring and summer in Thompson Woods, only two successfully reared two litters in the same year (1970 and 1973). There is no record of any female producing more than two consecutive litters. Smith (1967) reported one female gray squirrel productive for nine consecutive seasons. The Thompson Woods population departs from those described by Brown and Yeager (1945) and Allen (1943) which included old females typically producing two litters, and young-of-the-year one litter. Uhlig (1956) believed 20 to 30 percent of adult female gray squirrels bore two litters in an average year; and, in a peak year (1954), this proportion was 40 percent. Nixon and McClain (1975) found a 5-year average of 21.4 percent breeding both seasons.

Thirty litters prior to weaning averaged just under 2 young (1.97 young/litter); of 159 young captured, 147 were produced by 70 females. Using these data as representative of individual production in Thompson Woods, an average litter size of 2.10 is obtained. For this datum to be reliable it must be assumed that ingress or egress of unmarked young was zero or that discrepancies by season cancel rather than become additive. The two sets of data suggest that these assumptions were satisfactorily met.

Because many of the 159 young captured in Thompson Woods were 3 to 9 months old when age was first confirmed, comparison with other studies is difficult. However, Moran (1953) found an average litter to be 3.10 based on placental scars from a refuge population of females. Brown and Yeager (1945, p. 488) using counts of nestlings, fetuses, and placental scars obtained an average of 2.51 young per litter in oak-hickory upland habitat. Using similar criteria Allen (1943, p. 110) obtained an average of 3.02 young for 170 litters in Michigan.

Average litter size at or near parturition is not known for Thompson Woods; also, nestling mortality has not been evaluated. Eveland (1974, p. 66) considered his estimate of Thompson Woods litter size to be minimal and, therefore, comparable to that previously found for the fox squirrel. We question this interpretation. Thompson Woods is considered near optimum fox squirrel habitat with an abundance of tree cavities offering excellent protection and, in good mast years, an abundant source of food. Natural predators are scarce with dogs offering the greatest threat. Despite these favorable conditions, which would suggest a tendency for net ingress of new individuals, a low average litter size was observed. The predominance of litters having one or two young with only one litter in excess of three

young ever recorded suggests an abnormally low average litter size. The consistently low estimated seasonal averages, never surpassing 2.2 young per litter, further support this contention.

Seasonal difference in average litter size was not evident as five summer litters showed 2.2 young compared to 1.92 for 25 spring litters. According to Brown and Yeager (1945) seasonal difference in average litter size for both fox and gray squirrels was negligible. In contrast, adult gray squirrels in Ohio (Nixon and McClain 1975, p. 433) showed summer litters to be substantially larger than those in spring. Shorten (1951) and Smith (1967) reported larger summer litters for gray squirrels from both England and North Carolina.

From a management standpoint the number of young available for harvest and/or breeding is of importance. Depending on juvenile mortality, recruitment can contrast sharply with productivity indices such as average litter size, number of juveniles weaned, or proportion of females breeding. A standard measure of rearing success is the ratio of young to adult females in the succeeding breeding period (December). Data for Thompson Woods (Table 3) show for 1970, 1973, and 1975 relatively large numbers of young being recruited with the highest level in 1975. Three years were notably poor with negligible production occurring in 1974. Spring litters normally composed the bulk of recruits suggesting that any imposed harvest, even as early as the current 1 August opening in southern Illinois, would result in little loss of unborn or unweaned litters. Only in 1975 would an early harvest have been detrimental, possibly resulting in overharvest of an already depressed population.

Table 3. Rearing success among fox squirrels as indicated by sex and age ratios from December live-trapping, Thompson Woods, Southern Illinois University, 1968-75.

Year	Adult Males	Adult Females	Total Young	Young Females	Rearing Success: Total Young per adult female	Rearing Success: 2x Young Females per adult female
1968[a]	18	22	2	0	0.09	0.00
1969	16	20	17	7	0.85	0.70
1970	18	15	30	12	2.00	1.60
1971	26	21	15	8	0.71	0.76
1972	17	25	7	6	0.28	0.48
1973	16	20	20	11	1.00	1.10
1974	16	19	1	1	0.05	0.11
1975	11	12	26	16	2.17	2.67
Totals						
68-75	138	154	118	61	0.77	0.79
69-75	120	132	116	61	0.88	0.92

[a]Spring juveniles included as adults.

By assuming approximately equal susceptibility to live-trapping and gun harvest it is possible to compare data on rearing success in Thompson Woods with those from large samples based on hunter bat checks. The justification of this assumption reflects data collected in Michigan (Allen 1943, p. 127) where these two methods differed little in percentages of adults and juveniles found in a given area and year. Allen (1943) expected fall age ratios of about 60 percent young-of-the-year in a stable population. Assuming a 50 percent sex ratio among adults, a rearing success value of 3.0 (60 young per 20 adult females) would be anticipated. Actual values obtained from kill data on experimental areas in Michigan ranged from 27 to 79 percent juveniles; this reflects approximately 0.7 to 8.0 young per adult female. Kline (1964) noted several authors reporting a preponderence of juveniles in the harvest (Moran 1953, Packard 1956, Yeager 1959). Others, however, found equal age ratios (Allen 1952) or a majority of adults (Brown and Yeager 1945, Chapman 1938, Kidd 1955). Kline's (1964) data for nearly 10,000 Iowa fox squirrels reflected a juvenile:adult ratio of 1:17 to 1:00. Using an even sex ratio in the calculations, this corresponds to 2.34 young reared for each adult female. An average rearing success of 0.88 young per adult female over a 7-year period occurred in Thompson Woods. This low figure agrees with data previously presented on proportions of reproductively active adults and average litter size; it suggests that poor recruitment in Thompson Woods is a function of depressed production and not greatly influenced by juvenile mortality. Kline (1964) was convinced that many studies showing a high percentage of adults in fall populations and therefore a low rearing success, were a result of inaccurate aging techniques. Because most juveniles in Thompson Woods were enumerated and captured at a relatively early age and followed throughout their lives, Kline's

explanation is not applicable to our studies. There was substantial yearly variation in production and associated rearing success which may explain contrasting reports in the literature.

The importance of young squirrels produced in Thompson Woods to the total population is illustrated in Figure 2. It is readily apparent that in-woods production could not, at current levels, maintain a stable population. Substantial population declines and extended periods of reproductive inactivity may occur in unexploited populations occupying favorable habitats. The numbers of ingressing individuals exceeded production of young in 9 of 13 seasons even though, on the average, 6.69 individuals were added per season through ingress compared to 8.67 individuals produced. Ingressing

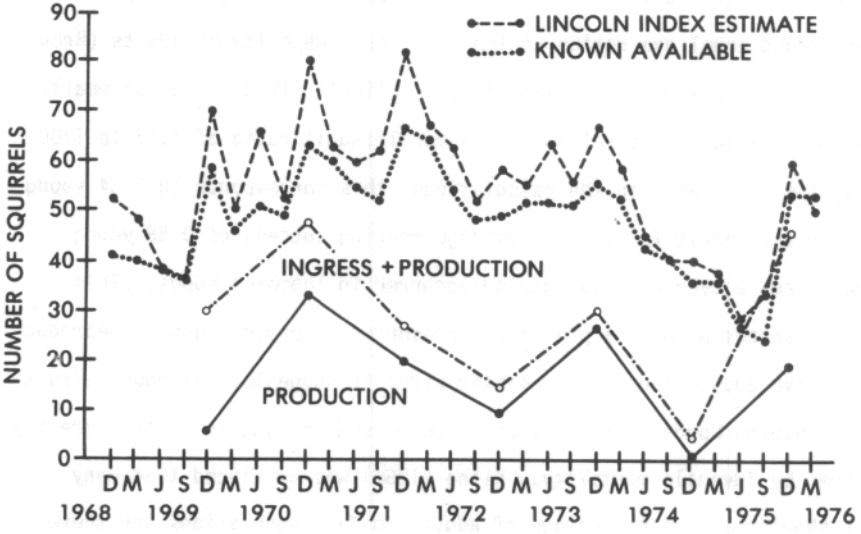

Figure 2. Trends in population size, by quarter, Thompson Woods, Southern Illinois University, 1968-76. Ingress and production for entire year recorded in December quarter.

squirrels (Figure 2) were largely adults which entered the woodlot during Falls having good mast crops. These data clearly indicate that immigration played a substantial role in the maintenance of population levels in Thompson Woods.

Evaluation of factors possibly responsible for the low reproductive rates observed in Thompson Woods was accomplished using a multiple regression analysis. Variables useful in distinguishing productive females from nonbreeders were related to some characteristic of the breeding season and not the individual. Adult females were more likely to be productive in spring seasons following abundant crops of tree seed. Spring production by adult females was also negatively correlated with the proportion of subadults in the population. It is interesting that individual characteristics such as chronological age, body weight, home range, and the incidence of external parasites or disease were of no value in distinguishing breeding from nonbreeding adults. The question of why some females remain unproductive in years of high reproductive activity or vice versa is still unanswered.

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