

# Effect of Harvest on Previously Unexploited Populations of Fox and Gray Squirrels

**Jacob L. Bowman,<sup>1</sup>** *Department of Wildlife and Fisheries, Box 9690, Mississippi State University, Mississippi State, MS 39762*

**Bobby T. Bond,** *Department of Wildlife and Fisheries, Box 9690, Mississippi State University, Mississippi State, MS 39762*

**Bruce D. Leopold,** *Department of Wildlife and Fisheries, Box 9690, Mississippi State University, Mississippi State, MS 39762*

**Michael J. Chamberlain,** *Department of Wildlife and Fisheries, Box 9690, Mississippi State University, Mississippi State, MS 39762*

**Jason M. Ross,<sup>2</sup>** *Department of Wildlife and Fisheries, Box 9690, Mississippi State University, Mississippi State, MS 39762*

---

*Abstract:* Effect of exploitation on sympatric southern squirrel populations has not been documented. Additionally, opportunities to study effects of harvest on unexploited populations are rare. Consequently, we investigated the effect of exploitation on a previously unharvested population of fox (*Sciurus niger*) and gray squirrels (*S. carolinensis*) on Twin Oaks Wildlife Management Area, Mississippi, from 1993–1998. We annually collected age, body morphometrics, color, sex, and species composition of harvested squirrels at voluntary check stations. A population decrease was documented for both species with stabilization occurring at different times ( $P \leq 0.001$ ). Fox squirrel age ratio changed following exploitation ( $P = 0.031$ ), but color and sex ratios did not ( $P > 0.05$ ). Gray squirrels exhibited no change in age, color, or sex ratios following exploitation ( $P > 0.05$ ). Body morphometrics of both species were affected by exploitation ( $P \leq 0.003$ ) and demonstrated a density dependent response. We hypothesized that exploitation reduced competition and allowed for increased body size. Fox squirrels exhibited reproductive compensation for exploitation, whereas gray squirrels did not. We hypothesized that gray squirrel compensation occurred through survival. Additionally, our data demonstrated that fox and gray squirrel populations in this study followed Caughley's (1985) partial compensation model.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 53:282–295

---

1. Present address: 255 Townsend Hall, Department of Entomology and Applied Ecology, University of Delaware, Newark, DE 19717–1303.

2. Present address: 340H Ayesbury Circle, Florida Game and Fresh Water Fish Commission, DeLand, FL 32720.

Fox and gray squirrels are popular small game animals in eastern North America (Flyger and Gates 1982) and Redmond (1953) found squirrels to be the most popular small game animal in Mississippi. Recently in Mississippi, Ross (1996) documented that squirrel hunting was second only to deer (*Odocoileus virginianus*) hunting as reflected by hunter-days. Although squirrels are popular game animals, relatively little is known about the effect of exploitation on their populations. However, Caughley (1985) stressed the importance of understanding the effect harvest has on any population.

Allen (1942) hypothesized that squirrel populations were affected by mast availability more than harvest rate; however, the effect of mast availability may be less pronounced with fox squirrels because agricultural crops alleviate complete dependence on mast. Mast crops have been linked to tree squirrel reproductive success in northern climates (Smith and Barkalow 1967; Nixon and McClain 1969, 1975; Barkalow et al. 1970; Gorman and Roth 1989; Koprowski 1991). Additionally, Nixon et al. (1975) documented that mast crops were extremely important to squirrel populations and speculated harvest was detrimental in poor mast crop years. However, southern squirrel populations, especially fox squirrels, may not be as affected by mast failures because of their more diverse diets (Weigl et al. 1989, Loeb and Moncrief 1993).

Several studies have examined the effect of exploitation on fox and gray squirrels (Uhlig 1956, Madson 1964, Mosby 1969, Nixon et al. 1974, Shugars 1986, Rhodes 1989). Early research suggested that harvest was not detrimental to gray squirrel populations, even at harvest levels of 50%–60% of the fall populations (Uhlig 1956, Madson 1964). Mosby (1969) demonstrated experimentally that 40% of the fall gray squirrel population could be harvested. Additionally, Mosby et al. (1977) described a “law of diminishing returns,” where hunter effort was positively correlated to squirrel densities. Thus, they believed hunters would cease harvest before populations were impacted negatively (Mosby et al. 1977). Some researchers have suggested that gray squirrels are under-harvested (Uhlig 1956, Madson 1964, Shugars 1986). Shugars (1986) in Maryland reported a 7%–9% annual mortality attributed to harvest with an annual mortality rate of 48%–54%. Similar mortality rates were documented in an unexploited gray squirrel population in North Carolina (Barkalow et al. 1970).

Compared to gray squirrels, over-harvest of fox squirrels has been documented. Nixon et al. (1974) reported detrimental effects of exploitation on fox squirrels with an average annual hunting mortality of 75.2% in a 22-ha woodlot in Ohio. Harvest mortality at such high levels caused the fox squirrel population to decline and increased immigration from adjacent woodlots (Nixon et al. 1974). An unexploited fox squirrel population in Illinois had an annual survival rate of >60% for adults (Nixon et al. 1986); thus, harvest on the woodlot in Ohio probably exceeded annual natural mortality for the population and thus was largely additive. In contrast to Nixon et al. (1974), Jordan (1971) documented no detrimental effects of an intensive fox squirrel harvest in a small, 27.7-ha woodlot in Pennsylvania.

Harvest is often considered compensatory for small mammals like squirrels (Caughley 1985). Kautz (1990) stated that for harvest to be sustainable, decreases in

natural mortality and/or increases in reproduction would have to compensate for losses resulting from harvest. Caughley (1985) described 2 types of compensatory models. Complete compensation occurs when harvest below some threshold has no effect on the population; thus, theoretically, harvested animals would have to succumb to another form of mortality (Caughley 1985, Burger et al. 1994). Partial compensation occurs when harvest at any level reduces the breeding population to below the unexploited density. Survival and/or reproduction are enhanced under partial compensation and the population achieves a greater potential rate of increase than when unexploited (Caughley 1985, Burger et al. 1994).

Mosby (1969) stated that exploitation can alter "the numerical and structural status of the population." Methods to detect exploitation effects have focused on measures of density, survival, age, and sex structures (Mosby 1969; Barkalow et al. 1970; Nixon et al. 1974, 1975; Shugars 1986; Rhodes 1989). Numerous studies have used age and sex ratios to determine the effect of exploitation on age and sex structure (Mosby 1969, Nixon et al. 1974, Shugars 1986, Rhodes 1989). Estimates of density and survival are more difficult to obtain because of logistical and financial constraints (Ross 1996). However, several researchers have documented high correlations ( $r > 0.80$ ) between squirrel harvest and density (Nixon et al. 1974, 1975; Shugar 1986). In addition to normal harvest parameters, Jacobson et al. (1979) noted the influence of botfly larvae (*Cuterebra emasculator*) on squirrel harvest; thus, documenting prevalence provides valuable information about when squirrel seasons should be initiated. Another consideration of exploitation is the effect on unique population characteristics, like melanism. Kiltie (1992) hypothesized that some adaptive advantage must be incurred by melanism; thus, knowing if exploitation adversely affects the frequency of melanism in the population is important.

Currently, a paucity of information exists on the effects of exploiting southern gray squirrel populations (Uhlig 1956, Mosby 1969, Shugars 1986) and although research from the Midwest and Northeast (Jordan 1971, Nixon et al. 1974, Rhodes 1989) has addressed fox squirrel exploitation, no information is available on the effects of exploiting southern fox squirrel populations. A decline in fox squirrel populations across the southeast mandates understanding all aspects of squirrel ecology, including the effect of exploitation (Edwards et al. 1989, Weigl et al. 1989, Loeb and Moncrief 1993). Thus, our study investigated the effect of exploitation on sympatric squirrel populations on an area with no hunting pressure prior to study initiation. We assumed a stable population prior to harvest. Our objectives were to determine if harvest affected (1) age, color or sex ratios of harvested squirrels and (2) mass or length of harvested squirrels.

We appreciate the cooperation of many hunters for graciously supporting this research. Funding was provided by the Mississippi Department of Wildlife, Fisheries, and Parks (special small game grant) and the Forest and Wildlife Research Center at Mississippi State University. We thank D. Brazil, B. Ballinger, S. Baker, D. Dew, and J. Fleeman for logistical assistance on the study area and for assistance in data collection. R. Bowman and T. Chamberlain assisted in data collection. L. W. Burger provided statistical advice and reviewed the manuscript. Approved for publication

as Journal Article Number WF-114 of the Forest and Wildlife Research Center, Mississippi State University. We thank L. W. Burger, S. Demarais and F. J. Vilella who reviewed early drafts of this manuscript.

## Methods

Twin Oaks Wildlife Management Area was a 2,302-ha bottomland hardwood forest acquired in 1992 by the Mississippi Department of Wildlife, Fisheries, and Parks as part of the U.S. Army Corps of Engineers Tennessee-Tombigbee Waterway Wildlife Mitigation Project. It was located in Sharkey County adjacent to Delta National Forest (Sunflower Wildl. Manage. Area). The area was composed of previously high-graded hardwood stands interspersed with agricultural fields. Hunter disturbance was minimal on the area prior to 1992 when it was privately owned. All existing roads were unimproved and access to interior roads was strictly limited.

Twin Oaks Wildlife Management Area was approximately 88% forested and 12% open areas. Dominant tree species included willow oak (*Quercus phellos*), sweetgum (*Liquidambar styraciflua*), overcup oak (*Q. lyrata*), bitter pecan (*Carya cordiformis*), American elm (*Ulmus americana*), boxelder (*Acer negundo*), ash (*Fraxinus* spp.), Nuttall oak (*Q. nuttallii*), water oak (*Q. nigra*), swamp chestnut oak (*Q. michauxii*), and sugarberry (*Celtis laevigata*). Other locally abundant tree species included bald cypress (*Taxodium distichum*), honey locust (*Gleditsia triacanthos*), black willow (*Salix nigra*), and black tupelo (*Nyssa sylvatica*). The midstory consisted of deciduous holly (*Ilex decidua*), swamp privet (*Ligustrum* spp.), and elm (*Ulmus* spp.). Dominant understory species included rattan vine (*Berchemia scandens*), wild grape (*Vitis* spp.), pepper vine (*Ampelopsis arborea*), poison ivy (*Rhus radicans*), greenbrier (*Smilax* spp.), and blackberry (*Rubus* spp.). Non-forested areas either remained in agriculture (50%) or were replanted in hardwoods (50%). Agricultural areas were planted in wheat, clover, corn, soybeans, milo, or millet. Planted hardwood species included willow oak, Nuttall oak, and water oak. Herbaceous species in replanted areas included Johnson grass (*Sorghum halepense*), sesbania (*Sesbania exaltata*), goldenrod (*Solidago* spp.), and ragweed (*Ambrosia* spp.).

Twin Oaks Wildlife Management Area was opened to hunting in 1993 and the previous owners stated that squirrel populations were not exploited for at least the last 10 years of private ownership. Two color-morphs of each species were present. In fox squirrels, there was a reddish color morph and a black melanistic morph. In gray squirrels, there was the standard salt and pepper "gray" color morph along with a black melanistic morph.

We collected hunter harvest data on opening weekend of squirrel season annually from 1993–1998. Color phase, sex, species, mass (g), body length (mm), age-class, lactation, and presence of botfly larvae data were collected at a voluntary hunter check station. Color phase information was not collected in 1993, and in 1997, due to data collection error, squirrel body length was not usable. Species identification was based on pelage, skull shape, ear shape, foot sole color, and dental formula. We

classified squirrels as adult, sub-adult, and juvenile based on tail pelage and secondary sexual characteristics (Day et al. 1980).

Each hunter was required to complete a hunter check card which included name, address, species (fox or gray squirrel) hunted, and number harvested. These cards provided estimates of total harvest for each day we checked squirrels. We obtained estimates of squirrels harvested/hunter-day by dividing squirrels harvested by total hunter-days. Estimates in 1993 and 1997 were based on hunters we actually checked because hunter check cards were not available. Additionally, hunter check cards were tallied for the adjacent Delta National Forest. This area, known as Sunflower Wildlife Management Area, has the same habitat as Twin Oaks Wildlife Management Area. Sunflower Wildlife Management Area was used for comparison because squirrels there had been harvested for >20 years. Only total squirrels harvested per hunting season for both species combined were available for Sunflower Wildlife Management Area; thus, these numbers were compared to Twin Oaks Wildlife Management Area hunting season totals combined for both species. Fox squirrels constituted >60% of the harvest in all years on Sunflower Wildlife Management Area (J. Fleeman, Miss. Dep. Wildl., Fish., and Parks, pers. commun.). Spearman rank correlation of year (1993–1998) and squirrels harvested/hunter-day were conducted to determine trends in squirrel abundance on each area (Conover 1980:254). Additionally, a 95% confidence interval was calculated for total squirrels harvested/hunter-day for Sunflower Wildlife Management Area from 1984–1998. Total squirrels harvested/hunter-day for Twin Oaks Wildlife Management Area from 1993–1998 were compared to the confidence interval to determine if Twin Oaks Wildlife Management Area squirrel harvest rates were different from those on Sunflower Wildlife Management Area.

We assumed that harvest during 1993 provided the baseline of an unexploited population for comparison to subsequent years with exploitation. Additionally, we tested all hypotheses separately for each species. We hypothesized that the ratio of species harvested would not change with time. This hypothesis was tested using a 2-way log-linear analysis with the main effects of species and year (Sokal and Rohlf 1981:731). This analysis was partitioned into separate tests representing individual degrees of freedom when we detected a lack of independence between the main effects (Sokal and Rohlf 1981:692).

We tested the hypothesis of no harvest effect on age, color, or sex ratios using a 2-way log-linear analysis with year and either age, color, or sex being the other main effect (Sokal and Rohlf 1981:731). We combined juveniles and sub-adults into a young-of-year class due to the low sample size of juveniles in all years except 1994. Log-linear analysis was partitioned into separate tests representing individual degrees of freedom when we detected a lack of independence between the main effects (Sokal and Rohlf 1981:692).

We hypothesized that harvest would not affect morphometrics of harvested squirrels. This hypothesis was tested using a completely randomized analysis of variance (ANOVA) on years (Petersen 1985:7). Assumptions for this analysis were tested using a Shapiro-Wilks statistic for normality (Conover 1980:363) and Levene's

test for homogeneity of variance (Milliken and Johnson 1992:19). We used only adults in this analysis because of assumption violations when including sub-adults. Additionally, length of fox squirrels and mass of gray squirrels were natural logarithm transformed to meet assumptions, and we conducted ANOVA or transformed variables (Sokal and Rohlf 1981:419). We investigated significant differences among years using Fisher's Protected Least significant Difference (FPLSD) multiple comparison procedure (Petersen 1985:77).

## Results

We collected data on 1,067 harvested squirrels from 1993–1998 (Table 1). Fox squirrels accounted for most ( $N=776$ ) of the harvested squirrels (Table 1) with gray squirrels accounting for the remaining 291 squirrels (Table 1). Numbers of hunters each year were 138, 78, 108, and 94 for 1994, 1995, 1996, and 1998, respectively. The density of hunters averaged 1 hunter/22 ha. Total squirrels harvested/hunter-day decreased across years ( $r_s=-0.99$ ,  $N=6$ ,  $P<0.001$ ) and stabilized in 1996 (Fig. 1). Gray squirrels harvested/hunter-day decreased from 1993 to 1994 ( $r_s=-0.97$ ,  $N=6$ ,  $P=0.001$ ), but stabilized over the remaining years of the study (Fig. 1). Fox squirrels had a similar decreasing trend ( $r_s=-0.99$ ,  $N=6$ ,  $P<0.001$ ), but stabilization did not occur until 1996 (Fig. 1). The total squirrels harvested/hunter-day was stable ( $r_s=0.09$ ,  $N=9$ ,  $P=0.872$ ) on Sunflower Wildlife Management Area from 1993–1998 (Fig. 2). A 95% confidence interval for total squirrels harvested/hunter-day on Sunflower Wildlife Management Area from 1984–1998 was 1.7–2.3. Total squirrels harvested/hunter-day on Twin Oaks Wildlife Management Area was above the confidence interval in 1993 (3.6) and 1994 (2.6), but within the interval remaining years (1995, 1.6; 1996, 1.9; 1997, 1.3; 1998, 1.6). Thus, squirrel abundance on Twin Oaks Wildlife Management Area stabilized at squirrels harvested per hunter-day levels similar to the adjacent Sunflower Wildlife Management Area (Fig. 2).

Lactation in harvested squirrels was uncommon. Low numbers of lactating females ( $N<5$ ) of both species in 3 of 6 years precluded using statistics. Additionally, botflies were uncommon in these populations. We found 4 botfly larvae in 3 fox squirrels and a single botfly larva on 1 gray squirrel.

The ratio of species harvested each year was not independent of year ( $\chi^2_5=16.164$ ,  $P=0.006$ ). A large shift in the ratio in 1995 and 1996 accounted for the variation. The partitioned log-linear tests detected no difference among years except for 1995 and 1996 (1993 and 1994:  $\chi^2_1=1.700$ ,  $P=0.192$ ; 1994 and 1995:  $\chi^2_1=1.510$ ,  $P=0.219$ ; 1995 and 1996:  $\chi^2_1=12.935$ ,  $P=0.001$ ; 1996 and 1997:  $\chi^2_1=1.076$ ,  $P=0.299$ ; 1997 and 1998:  $\chi^2_1=0.031$ ,  $P=0.859$ ).

Fox squirrel sex ratio was independent of year ( $\chi^2_5=1.262$ ,  $P=0.939$ ). Age ratio for fox squirrels was not independent of years ( $\chi^2_5=12.293$ ,  $P=0.031$ ). The partitioned log-linear tests detected differences among years in 1994–1996 (1993 and 1994:  $\chi^2_1=0.012$ ,  $P=0.912$ ; 1994 and 1995:  $\chi^2_1=5.994$ ,  $P=0.014$ ; 1995 and 1996:  $\chi^2_1=10.693$ ,  $P=0.001$ ; 1996 and 1997:  $\chi^2_1=2.167$ ,  $P=0.141$ ; 1997 and 1998:  $\chi^2_1=0.078$ ,  $P=0.780$ ). A bimodal reproductive pulse documented in 1994 accounts

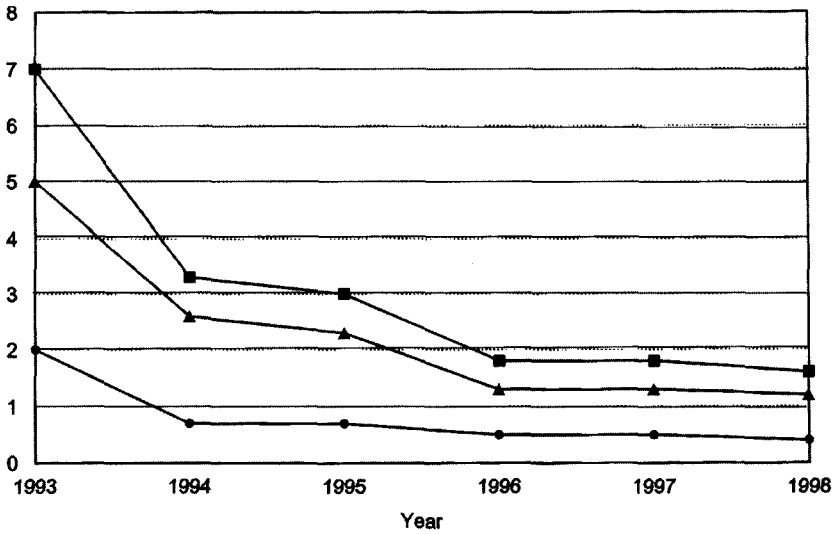
**Table 1.** Sex and age of hunter harvested fox and gray squirrels on Twin Oaks Wildlife Management Area, Mississippi, 1993–1998.

Year	Sex	Fox Squirrel					Gray Squirrel					Grand Total <sup>c</sup>
		Adult	Sub-adult	Juvenile	Total <sup>a</sup>	Age Ratio <sup>b</sup>	Adult	Sub-adult	Juvenile	Total <sup>a</sup>	Age Ratio <sup>b</sup>	
1993	Female	83	30	6	239	1.0:2.6	27	15	4	91	1.0:1.8	330
	Male	65	53	2			12	30	3			
1994	Female	36	17	14	136	1.0:2.7	14	5	5	39	1.0:2.3	175
	Male	49	5	15			8	3	4			
1995	Female	21	22	1	101	1.0:1.9	4	6	0	20	1.0:2.0	121
	Male	26	31	0			6	4	0			
1996	Female	29	22	6	117	1.0:3.2	10	4	11	63	1.0:1.9	180
	Male	51	7	2			20	10	8			
1997	Female	23	17	3	89	1.0:2.4	12	2	3	37	1.0:2.8	126
	Male	29	14	3			12	6	2			
1998	Female	21	21	2	94	1.0:2.3	9	7	4	41	1.0:1.5	135
	Male	32	13	5			5	12	4			

a. Total number of squirrels by species and year checked by hunters.

b. Young-of-year (sub-adult and juvenile) to adult ratio.

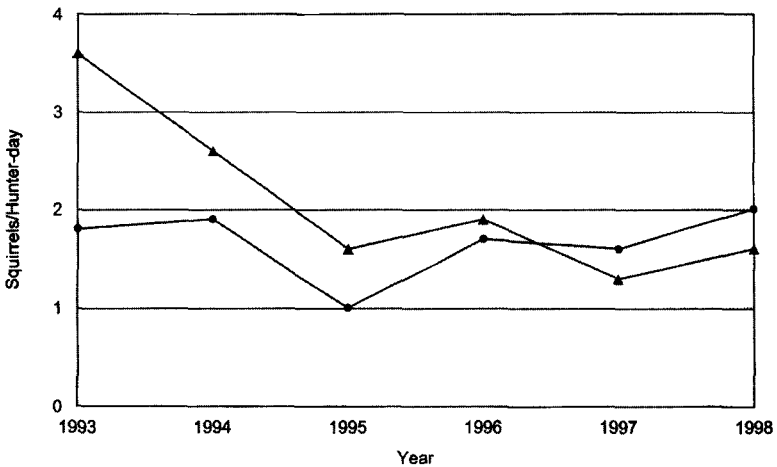
c. Total number of fox and gray squirrels checked by hunters for a particular year.



**Figure 1.** Total (□), fox (△) and gray (○) squirrels harvested/hunter-day on opening weekend of squirrel season on Twin Oaks Wildlife Management Area, Mississippi, 1993–1998.

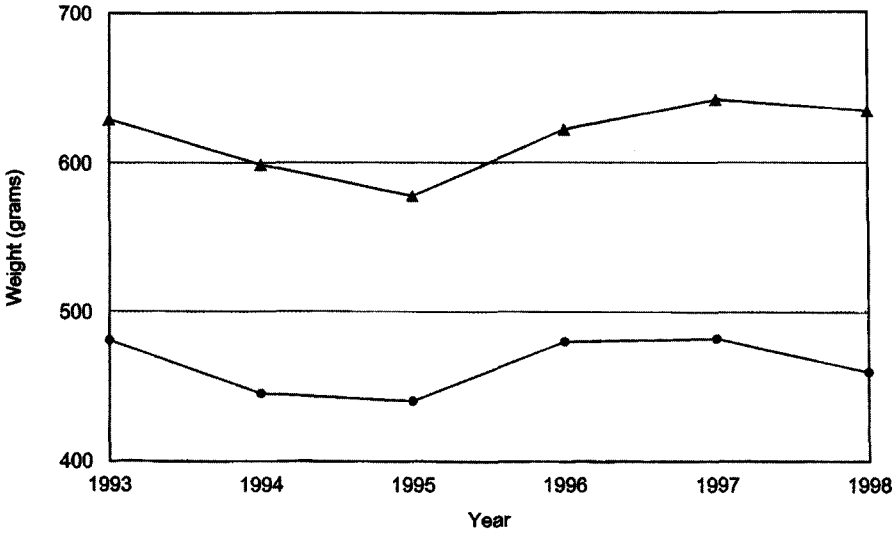
for differences in those years (Table 1). Black fox squirrels were harvested every year (1994,  $N=42$ ; 1995,  $N=43$ ; 1996,  $N=29$ ; 1997,  $N=26$ ; 1998,  $N=29$ ). The color ratio was independent of year ( $\chi^2_4=8.267$ ,  $P=0.082$ ).

Mass (g) of fox squirrels differed among years ( $F=15.55$ ,  $P<0.001$ ) (Fig. 3). FPLSD grouped means into 4 groups. The first group consisted of 1997 ( $N=52$ ,



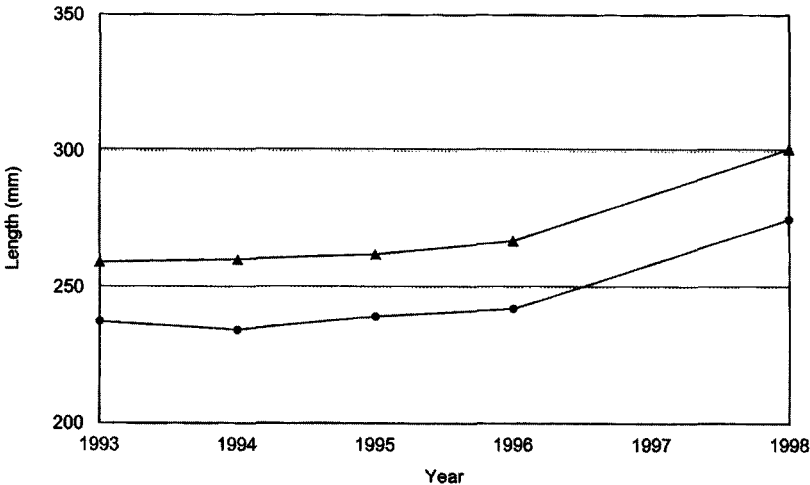
**Figure 2.** Comparison of total squirrels harvested/hunter-day for entire squirrel season on Sunflower (○) and Twin Oaks (△) Wildlife management Areas, Mississippi, 1990–1998.





**Figure 3.** Fox (Δ) and gray (○) squirrel weights (g) for Twin Oaks Wildlife Management Area, Mississippi, 1993–1998.

$\bar{x}=642$ ,  $SD=7$ ), 1998 ( $N=53$ ,  $\bar{x}=634$ ,  $SD=7$ ), and 1993 ( $N=148$ ,  $\bar{x}=629$ ,  $SD=4$ ). The second group consisted of 1998, 1993, and 1996 ( $N=80$ ,  $\bar{x}=622$ ,  $SD=5$ ). The years 1994 ( $N=85$ ,  $\bar{x}=599$ ,  $SD=5$ ) and 1995 ( $N=47$ ,  $\bar{x}=578$ ,  $SD=8$ ) were each grouped independently. Length (mm) of fox squirrels differed among years ( $F=103.36$ ,  $P<0.001$ ) (Fig. 4). FPLSD grouped means into 3 groups. The largest mean lengths were observed in 1998 ( $N=53$ ,  $\bar{x}=301$ ,  $SD=2$ ) and 1996 ( $N=80$ ,



**Figure 4.** Fox (Δ) and gray (○) squirrel body lengths (mm) for Twin Oaks Wildlife Management Area, Mississippi, 1993–1998.

$\bar{x}=267$ ,  $SD=2$ ), which were grouped independently. The final group with the lowest means was 1995 ( $N=47$ ,  $\bar{x}=263$ ,  $SD=2$ ), 1994 ( $N=85$ ,  $\bar{x}=260$ ,  $SD=1$ ), and 1993 ( $N=148$ ,  $\bar{x}=259$ ,  $SD=1$ ).

Gray squirrel sex ( $\chi^2_5=4.908$ ,  $P=0.427$ ) and age ( $\chi^2_5=9.582$ ,  $P=0.088$ ) ratios were independent of year. Black gray squirrels were harvested in 1994 ( $N=7$ ) and 1996 ( $N=9$ ). The low occurrence of black gray squirrels in the harvest precluded use of statistics.

Mass (g) of gray squirrels differed among years ( $F=3.84$ ,  $P=0.003$ ) (Fig. 3). FPLSD grouped means into 2 groups. The first group consisted of 1997 ( $N=24$ ,  $\bar{x}=482$ ,  $SD=8$ ), 1993 ( $N=39$ ,  $\bar{x}=481$ ,  $SD=7$ ), 1996 ( $N=29$ ,  $\bar{x}=480$ ,  $SD=9$ ), and 1998 ( $N=14$ ,  $\bar{x}=459$ ,  $SD=9$ ). The second group with the lowest means was 1994 ( $N=22$ ,  $\bar{x}=445$ ,  $SD=11$ ) and 1995 ( $N=10$ ,  $\bar{x}=440$ ,  $SD=14$ ). Length (mm) of gray squirrels differed among years ( $F=30.62$ ,  $P<0.001$ ) (Fig. 4). FPLSD grouped means into 3 groups. The largest mean was 1998 ( $N=14$ ,  $\bar{x}=275$ ,  $SD=3$ ), which was grouped independently. The second group consisted of 1996 ( $N=30$ ,  $\bar{x}=242$ ,  $SD=2$ ), 1995 ( $N=10$ ,  $\bar{x}=239$ ,  $SD=4$ ), and 1993 ( $N=39$ ,  $\bar{x}=237$ ,  $SD=2$ ). The group with the lowest means consisted of 1995, 1993, and 1994 ( $N=22$ ,  $\bar{x}=234$ ,  $SD=2$ ).

## Discussion

Allen (1942) reported that squirrel populations were affected more by mast availability than harvest, except in bottomland forests. Nixon et al. (1975) documented detrimental effects of harvest in poor mast crop years for an upland area. In contrast, Nixon et al. (1986) documented no effect of mast crop on fox squirrel demographics. Mosby (1969) reported "little or no measurable effect" of poor mast crop on gray squirrel populations. Southern squirrel populations were less sensitive to mast failures because of their greater diet diversity (Weigl et al. 1989, Loeb and Moncrief 1993). Additionally, with  $>6$  species of hard mast and abundant soft mast on our study area, we believe a failure was not probable and agency personnel did not record any years with low mast production (J. Fleeman, Miss. Dep. Wildl., Fish., and Parks, pers. commun.). We believe the high species richness of hard mast provided abundant mast every year. Weigl et al. (1989) cautioned managers to closely monitor harvests because they could have a larger impact on squirrel populations than mast availability.

Our data on population parameters supported past research, which determined that harvest had no effect on gray squirrel populations (Uhlig 1956, Madson 1964, Mosby 1969). We did not document the harvest pressure of Shugars (1986), 1 hunter per 4–10 ha. The "law of diminishing returns" (Mosby et al. 1977) may have acted here. Given that gray squirrel abundance was lower than fox squirrels, hunters likely targeted fox squirrels and harvested gray squirrels incidentally. Our research contrasted Nixon et al. (1974) who documented detrimental effects of exploitation on fox squirrels. However, our population occupied a much larger area and we did not record hunter densities comparable to Nixon et al. (1974), 1 hunter per 1.4–5.5 ha. Our results were similar to Jordan (1971) who reported no detrimental effects of fox squirrel harvest.

Population sizes of fox and gray squirrels were most likely not equal. Fox squirrels were harvested more frequently every year, likely a result of higher abundance. Gray squirrels accounted for 20%–30% of harvested squirrels most years except 1995 when they represented only 17% of the harvest. A possible hypothesis for the decrease in gray squirrels in 1995 was fox squirrels experienced extensive recruitment that may have provided more fox than gray squirrels for harvest. Another hypothesis for population difference was interspecific competition. Brown and Batzli (1985) could not demonstrate interspecific competition in fox and gray squirrels; even when densities were lowered, gray squirrels did not out-compete fox squirrels. Fox and gray squirrels most likely coexist by niche partitioning, resulting from differential use of habitat and nest trees (Edwards et al. 1998).

Exploitation did not affect color ratios. Melanism in squirrels is poorly understood (Kiltie 1992). Melanistic squirrels must be “neutral” or incur some adaptative advantage over common color morph squirrels, or melanism would be selected against and disappear from the population (Kiltie 1992). However, the lack of knowledge on melanism necessitates that we ensure continued existence of this melanistic phase, in so much as we insure that harvest is not detrimental to melanistic squirrels. No decrease in melanism was noted among harvested squirrels; thus, harvest did not adversely affect melanistic squirrels.

Gray squirrels showed no effect of exploitation on age or sex ratios, but extensive variation in these ratios did occur. We detected no clear trend in either of these parameters. Gray squirrel compensation must have occurred in survival rates because no effect on reproduction was documented. Mosby (1969) documented similar results of no difference in sex ratios between exploited and unexploited populations. However, he did not document any effect on reproduction (Mosby 1969). Additionally, Nixon et al. (1975) reported no change in sex ratios, although they did document that as gray squirrel populations increased the proportion of adults decreased.

In contrast, fox squirrels exhibited a density dependent reproductive response to exploitation. An initial increase in reproduction was documented in 1994 with a bimodal reproductive pulse; in all other years juveniles accounted for a small percentage of the young-of-year age-class. Additionally, in 1995, an increase in the young-of-year age-class can be attributed to the large bimodal pulse in 1994, and increased adults in 1996 was attributed to the large reproductive pulse in 1994 and 1995. Reproduction stabilized in 1997 and 1998 at levels slightly higher than pre-exploitation, but these numbers demonstrated reproductive compensation. However, our data were not sufficient to show a compensatory response in survival. Past research has documented no change in sex ratios (Nixon et al. 1975, 1986). Additionally, Nixon et al. (1974) documented changes in age ratios as in our study; however, their young-of-year to adult ratio was 6.46:1.0 which was much higher than in our study (1.0:9–3.2) (Nixon et al. 1974). Nixon et al. (1974) documented harvest mortality at 75.2% and attributed the increased proportion of young-of-year resulted from not only increased reproduction, but also immigration.

Both species demonstrated an effect of exploitation on morphometrics. Mass declined initially, probably due to removal of older aged adults; thus, remaining

adults would be younger and may not have reached full physical development. Squirrel masses increased during the study until no difference existed between unexploited masses in 1993 and those at the end of the study. We hypothesized, even with high population turnover, that at lower densities, younger aged adult squirrels could obtain weights comparable to older aged adult squirrels at the beginning of the study because of reduced competition. Lengths of squirrels increased throughout the study as a result of reduced competition. Why lengths of squirrels did not stabilize like masses did was unclear. Increased size could lead to early maturation, resulting in increased population reproductive potential, demonstrating a density dependent response (McCullough 1990); however, our data were insufficient to demonstrate that early maturation occurred.

We hypothesized that squirrel populations on Twin Oaks Wildlife Management Area followed Caughley's (1985) partial compensation model based on our documented decline in squirrel abundance pre- to post-exploitation. Nixon et al. (1974) found a significant correlation between pre-season squirrel density and squirrel harvest; thus, we believe that the abundance of squirrels on Twin Oak Wildlife Management Area was reduced. Additionally, we found that fox squirrels compensated reproductively initially but stabilized 4 years after exploitation (McCullough 1990). Kautz (1990) hypothesized that compensation would occur by density dependent decreases in natural mortality and/or increases in reproduction. In contrast to fox squirrels, gray squirrels showed no reproductive compensation and we hypothesized that compensation occurred in natural mortality. Morphometrics demonstrated density dependent response to harvest. The effect of reduced competition on morphometrics further supports our hypothesis that these squirrel populations exhibit partial compensation.

Squirrels harvested/hunter man-day on Twin Oaks Wildlife Management Area declined to a nearly identical level as the adjacent Sunflower Wildlife Management Area. If we had delayed data collection for even 2 years, we would not have detected any differences in the 2 areas. A comparison of the areas after several years would have led to a conclusion that squirrel populations on Twin Oaks follow the complete compensation model. Research needs to follow unexploited populations during the first years of exploitation, as initial population declines and reproductive responses may not be detectable after several years and incorrect conclusions may result.

### **Management Implications**

In most southern states squirrel season is structured to avoid harvesting lactating females and squirrels parasitized by botfly larvae (Jacobson et al. 1979, Jacobson et al. 1981). Squirrel season opens in mid-October in central Mississippi. Our results demonstrate that under current regulations, prevalence of botfly larvae and lactating females are extremely low; thus, the current season structure appears to be achieving desired results.

Our data demonstrate that squirrel populations are sustainable at current levels of exploitation and that they exhibit partial compensatory responses as described by

Caughley (1985). We found a decrease in the squirrel population after exploitation, followed by a stabilization of the population at a lower level. Research needs to investigate the effect of reduced harvest levels on an unexploited population. We postulated that if harvest was restricted to a lower level, we could have maintained a higher squirrel population and harvest rates with stabilization occurring at some point above that of our study. Additionally, we concur with Mosby et al. (1977) that a law of diminishing returns likely occurs as hunter effort decreases as squirrel populations decrease.

## Literature Cited

- Allen, D. L. 1942. Populations and habits of the fox squirrel in Allegan County, Michigan. *Am. Midl. Nat.* 27:338–379.
- Barkalow, F. S., Jr., R. B. Hamilton, and R. F. Soots, Jr. 1970. The vital statistics of an unexploited gray squirrel population. *J. Wildl. Manage.* 34:489–500.
- Brown, B. W. and G. O. Batzli. 1985. Field manipulations of fox and gray squirrel populations: how important is interspecific competition? *Can. J. Zool.* 63:2134–2140.
- Burger, L. W., Jr., E. W. Kurzejeski, L. D. Vangilder, T. V. Dailey, and J. H. Schulz. 1994. Effects of harvest on population dynamics of upland gamebirds: Are bobwhite the model? *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 59:466–476.
- Caughley, G. 1985. Harvesting of wildlife: past, present, and future. Pages 3–14 in S. L. Beasom and S. F. Robertson, eds. *Game Harvest Management*. Caesar Kleberg Wildl. Res. Inst., Kingsville, Texas.
- Conover, W. J. 1980. *Practical nonparametric statistics*. Second ed. John Wiley and Sons, New York. 493pp.
- Day, G. I., S. D. Schemnitz, and R. D. Taber. 1980. Capturing and marking wild animals. Pages 61–68 in S. D. Schemnitz, ed. *Wildlife Management Techniques Manual*. The Wildl. Soc., Washington, D.C.
- Edwards, J. W., C. D. Guynn, Jr., and M. R. Lennartz. 1989. Habitat use by southern fox squirrel in coastal South Carolina. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 43:337–345.
- , D. G. Heckel, and D. C. Guynn, Jr. 1998. Niche overlap in sympatric populations of fox and gray squirrels. *J. Wildl. Manage.* 62:354–363.
- Flyger, V. and J. E. Gates. 1982. Fox and gray squirrels. Pages 209–229 in J. A. Chapman and G. A. Feldhamer, eds. *Wild Mammals of North America: Biology, Management, and Economics*. Johns Hopkins Univ. Press, Baltimore, Md.
- Gorman, O. T. and R. R. Roth. 1989. Consequences of a temporally and spatially variable food supply for an unexploited gray squirrel (*Sciurus carolinensis*) population. *Am. Midl. Nat.* 12:41–60.
- Jacobson, H. A., D. C. Guynn, and E. J. Hackett. 1979. Impact of the botfly on squirrel hunting in Mississippi. *Wildl. Soc. Bull.* 7:46–48.
- , ———, M. S. Hetrick, and D. C. Guynn. 1981. Prevalence of *Cuterebra emasculator* in squirrels in Mississippi. *J. Wildl. Diseases* 17:79–87.
- Jordan, J. S. 1971. Yield from an intensively hunted population of eastern fox squirrels. Northeast. For. Exp. Sta., Upper Darby, Pa. USDA For. Serv. Res. Pap. NE-186. 8pp.
- Kautz, J. E. 1990. Testing for compensatory responses to removals from wildlife populations. *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 55:527–533.

- Kiltie, R. A. 1992. Camouflage comparisons among fox squirrels from the Mississippi River Delta. *J. Mammal.* 73:906–913.
- Koprowski, J. L. 1991. Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. *J. Mammal.* 72:367–372.
- Loeb, S. C. and N. D. Moncrief. 1993. The biology of fox squirrels (*Sciurus niger*) in the southeast: a review. Pages 1–19 in J. W. Edwards and P. A. Tappe, eds. Proceedings of the Second Symposium on Southeastern Fox Squirrel. Va. Mus. Nat. Hist. Spec. Publ. 1.
- Madson, J. 1964. Gray and fox squirrels. Olin Mathieson Chemical Corporation, East Alton, Illinois. 112pp.
- McCullough, D. R. 1990. Detecting density dependence: filtering the baby from the bathwater. *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 55:534–543.
- Milliken, G. A. and D. E. Johnson. 1992. *Analysis of messy data, volume 1: designed experiments.* Chapman and Hall, New York. 473 pp.
- Mosby, H. S. 1969. The influence of hunting on the population dynamics of a woodlot gray squirrel population. *J. Wildl. Manage.* 33:59–73.
- , R. L. Kirkpatrick, and J. O. Newell. 1977. Seasonal vulnerability of gray squirrels to hunting. *J. Wildl. Manage.* 41:284–289.
- Nixon, C. M., R. W. Donohoe, and T. Nash. 1974. Overharvest of fox squirrels from two woodlots in western Ohio. *J. Wildl. Manage.* 38:67–80.
- , L. P. Hansen, and S. P. Havera. 1986. Demographic characteristics of an unexploited population of fox squirrels (*Sciurus niger*). *Can. J. Zool.* 64:512–521.
- and M. W. McClain. 1969. Squirrel population decline following a late spring frost. *J. Wildl. Manage.* 33:353–357.
- and M. W. McClain. 1975. Breeding seasons and fecundity of female gray squirrels in Ohio. *J. Wildl. Manage.* 39:426–438.
- , M. W. McClain, and R. W. Donohoe. 1975. Effects of hunting and mast crops on a squirrel population. *J. Wildl. Manage.* 39:1–25.
- Peterson, R. G. 1985. *Design and Analysis of Experiments.* Marcel Dekker, Inc., New York. 426pp.
- Redmond, H. R. 1953. Analysis of gray squirrel breeding studies and their relation to hunting season, gunning pressure, and habitat conditions. *Trans. N. Am. Wildl. Conf.* 18:378–389.
- Rhodes, M. N. 1989. Effects of exploitation on population parameters of fox squirrels and gray squirrels: a hunting experiment and computer model. Ph.D. Diss., Univ. Mo., Columbia. 156pp.
- Ross, J. M. 1996. Habitat components and relative abundance of the fox squirrel in relation to forest management practices. M. S. Thesis, Miss. State University, Mississippi State, Miss. 111pp.
- Shugars, J. C. 1986. Harvest analysis of a Maryland gray squirrel population. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 40:382–388.
- Smith, N. B. and F. S. Barkalow, Jr. 1967. Precocious breeding in the gray squirrel. *J. Mammal.* 48:328–330.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry.* Second ed. W. H. Freeman and Co., San Francisco. 887pp.
- Uhlfg, H. G. 1956. The gray squirrel in West Virginia. *Conserv. Comm. W. Va., Charleston.* 83pp.
- Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. *Tall Timbers Res. Sta., Bull.* 24. 93pp.