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Notes and Discussion

Differential Estimates of Southern Flying Squirrel (Glaucomys volans) Population Structure Based on Capture Method

ABSTRACT.—It is commonly assumed that population estimates derived from trapping small mammals are accurate and unbiased or that estimates derived from different capture methods are comparable. We captured southern flying squirrels (*Glaucomys volans*) using two methods to study their effect on red-cockaded woodpecker (*Picoides borealis*) reproductive success. Southern flying squirrels were captured at and removed from 30 red-cockaded woodpecker cluster sites during March to July 1994 and 1995 using Sherman traps placed in a grid encompassing a red-cockaded woodpecker nest tree and by hand from red-cockaded woodpecker cavities. Totals of 195 (1994) and 190 (1995) red-cockaded woodpecker cavities were examined at least three times each year. Trappability of southern flying squirrels in Sherman traps was significantly greater in 1995 (1.18%; 22,384 trap nights) than in 1994 (0.42%; 20,384 trap nights), and capture rate of southern flying squirrels in cavities was significantly greater in 1994 (22.7%; 502 cavity inspections) than in 1995 (10.8%; 555 cavity inspections). However, more southern flying squirrels were captured per cavity inspection than per Sherman trap night in both years. Male southern flying squirrels were more likely to be captured from cavities than in Sherman traps in 1994, but not in 1995. Both male and female juveniles were more likely to be captured in cavities than in traps in both years. In 1994 males in reproductive condition were more likely to be captured in cavities than in traps and in 1995 we captured significantly more reproductive females in cavities than in traps. Our data suggest that population estimates based solely on one trapping method may not represent true population size or structure of southern flying squirrels.

INTRODUCTION

Live-trapping often is used to obtain information about population size and structure of small mammals. It is commonly assumed that estimates of population parameters based on data obtained in this way are unbiased. However, differential capture rates of rodents have been documented between, among and within snap traps, box traps and pitfall traps (*e.g.*, Williams and Braun, 1983; Szaro *et al.*, 1988; Slade *et al.*, 1993; O'Farrell *et al.*, 1994), as well as trap height (Engel *et al.*, 1992; Risch and Brady, 1996; Taylor and Lowman, 1996; Loeb *et al.*, 1999; Laakkonen, 2003). Due to variation in capture rates among age and sex classes, estimates of population structure may also be biased among trapping methods (*e.g.*, Boonstra and Krebs, 1978; Beacham and Krebs, 1980; Slade *et al.*, 1993; Laakkonen, 2003). Because age and sex ratios are important for assessing population dynamics and the effects of management on populations, accurate estimates of population structure are critical to understanding animal population ecology (Meffe and Carroll, 1997).

Sherman livetraps (H.B. Sherman Traps, Inc, Tallahassee FL[1]) often are used to capture southern flying squirrels (*Glaucomys volans*). Another method is capturing southern flying squirrels from tree cavities or nest boxes where they nest and den (Sonenshine *et al.*, 1973). Southern flying squirrels are captured in traps during their nightly foraging and commuting activities, whereas nest box or cavity captures represent daytime den use. Thus, captures of southern flying squirrels from traps and cavities may reflect different segments of the population, and studies using different capture methods may not be comparable. As part of an experiment that examined the effects of southern flying squirrels on the endangered red-cockaded woodpecker's (*Picoides borealis*) reproductive success (Laves and Loeb, 1999), we captured southern flying squirrels with Sherman live traps and cavity searches. Herein, we compare capture rates and estimates of population structure for southern flying squirrels captured in Sherman

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service

live traps with those captured in cavities to determine whether estimates based on these two capture methods differed, thus, are biased.

STUDY AREA AND METHODS

Our study was conducted in the Carolina Sandhills National Wildlife Refuge (CSNWR), Chesterfield County, South Carolina. The 18,600 ha refuge is in a transition zone between the Atlantic Coastal Plain and Piedmont Plateau physiographic provinces. Average minimum and maximum monthly temperatures range from 0.1 C and 12.0 C in January to 20.8 C and 32.6 C in July (SERCC, 2005). Average monthly rainfall ranges from 7.3 cm in April to 14.6 cm in July. Average minimum temperatures during the study periods ranged from 6.8 C to 21.4 C in 1994 and from 6.3 C to 21.6 C in 1995. Average maximum temperatures ranged from 20.7 C to 31.3 C in 1994 and from 20.6 C to 33.2 C in 1995. Except for March, monthly rainfall was also similar between years. In March 1994 there were 12.9 cm of rain whereas in March 1995 there were only 4.9 cm.

Approximately 85% of the refuge is forested in longleaf pine (*Pinus palustris*); the remainder is in loblolly pine (*P. taeda*), slash pine (*P. elliottii*) and pond pine (*P. serotina*). Oaks (*Quercus* spp.) are the dominant deciduous species and are common along streams and on lower slopes. The CSNWR was actively managed for red-cockaded woodpeckers before and during the study. Management activities included prescribed dormant season burns every 3–5 y to control understory vegetation and mechanical removal of midstory hardwoods in some areas. However, activities were limited during the red-cockaded woodpecker breeding season and were conducted on only a portion of the clusters each year.

We captured and removed southern flying squirrels from 30 red-cockaded woodpecker cavity tree clusters, which included approximately 190 red-cockaded woodpecker cavities, during March–early July 1994 and 1995. A cluster is the aggregation of cavity trees used by a group of red-cockaded woodpeckers (Walters, 1990). Before and during the red-cockaded woodpecker breeding season, we climbed all RCW cavity trees within a 500 m radius of a red-cockaded woodpecker nest cavity at least once a month and removed southern flying squirrels from all cavities with a mechanical pick-up tool (MM Manufacturing, Davis, OK). Cavity heights ranged from 1.2 m to 19.5 m above ground level. Within each cluster, we also placed 16 collapsible aluminum Sherman live traps (7.5 by 9.0 by 25.5 cm) enclosed in horizontal wooden trap sleeves, 1.5 m above ground on the boles of trees, in a 4 by 4 grid with approximately 50 m spacing. Our trapping grids were situated to include the red-cockaded woodpecker nest tree. We trapped on a nine night open, five night closed schedule. Traps were baited with peanut butter and examined daily. We recorded sex, age and reproductive status of all captured southern flying squirrels. We classified animals as juvenile if they weighed $\leq$37 g, subadult if they weighed 38–55 g and adult if they weighed >55 g (Sollberger, 1943; Linzey and Linzey, 1979; Riter and Vallowe, 1978). Reproductive condition of females was determined by the appearance of the vulva and mammae; reproductive condition of males was based on size and position of the testes. Because this was a removal study with possible beneficial effects on the endangered red-cockaded woodpecker, we euthanized all flying squirrels by cervical dislocation (Clemson University AUP # 93-053). We defined trappability as either the number of southern flying squirrels captured per trap-night or number of southern flying squirrels captured per cavity inspection. One trap-night was equivalent to one trap opened for one night. We used likelihood ratio tests (PROC FREQ; SAS, 1999) to test the null hypotheses that trappability of southern flying squirrels did not differ between capture methods and years, and between age, sex and reproductive classes. We used chi-square goodness-of-fit tests to determine whether sex ratios (male:female) differed significantly from a 1:1 ratio.

RESULTS

We examined 195 red-cockaded woodpecker cavities in 1994 and 190 red-cockaded woodpecker cavities in 1995. More southern flying squirrels were captured per cavity inspection than per Sherman trap-night in both years. In 1994, 86 southern flying squirrels were captured in 20,384 trap nights (0.42% trap success) and 114 southern flying squirrels were removed from cavities during 502 cavity inspections (22.7% success). In 1995, 261 southern flying squirrels were captured in 22,208 trap-nights

(1.18%) and 60 southern flying squirrels were removed during 555 cavity inspections (10.8%). Trappability of southern flying squirrels in Sherman traps was significantly greater in 1995 than in 1994 ($\chi^2 = 78.69$, df = 1, P = 0.001) and trappability of southern flying squirrels from cavities was significantly greater in 1994 than in 1995 ($\chi^2 = 26.07$, df = 1, P = 0.001).

In 1994 sex ratios of adult animals captured in traps or cavities did not differ significantly from a 1:1 ratio ($\chi^2 = 1.47$, df = 1, P = 0.22 and $\chi^2 = 2.88$, df = 1, P = 0.09, respectively). However, males and females differed in their propensities to be captured in traps and cavities ($\chi^2 = 4.26$, df = 1, P = 0.04). Males were more likely to be captured from cavities (58.6%) than in traps (41.4%) and females were more likely to be captured in traps (59.1%) than from cavities (40.9%). In 1995, 83.8% of the adult males and 82.0% of the adult females were captured in traps and males and females did not differ significantly in their propensities to be captured in traps and cavities ($\chi^2 = 0.12$, df = 1, P = 0.73). The sex ratio (male:female) of adult southern flying squirrels based on trap captures was 1.77:1 which differed significantly from a 1:1 ratio ($\chi^2 = 15.52$, df = 1, P < 0.0001). The sex ratio of adult southern flying squirrels based on cavity captures was 1.56:1. Although this ratio also was skewed towards males, it did not differ significantly from 1:1 ($\chi^2 = 1.98$, df = 1, P = 0.16).

Estimates of age ratios differed significantly between capture methods for females in both years ($\chi^2 = 14.68$, df = 2, P = 0.0006 and $\chi^2 = 8.68$, df = 2, P = 0.01 for 1994 and 1995, respectively) and for males in 1995 ($\chi^2 = 4.85$, df = 2, P = 0.09 and $\chi^2 = 7.24$, df = 2, P = 0.03, for 1994 and 1995, respectively). Juveniles were far more likely to be captured in cavities than in traps (Fig. 1). When juveniles were excluded from the analyses, estimates of age ratios based on captures from traps and cavities did not differ for either males or females in both years (all P $\geq$ 0.12).

In some instances the proportion of reproductive individuals captured in traps differed from the proportion captured in cavities (Fig. 2). In 1994 males in reproductive condition were more likely to be captured from cavities than in traps ($\chi^2 = 5.63$, df = 1, P = 0.02), but no differences were evident in 1995 ($\chi^2 = 0.0032$, df = 1, P = 0.96). Reproductive females were more likely to be captured from red-cockaded woodpecker cavities than in traps in 1995 ($\chi^2 = 4.03$, df = 1, P = 0.04), but not in 1994 ($\chi^2 = 2.13$, df = 1, P = 0.14).

DISCUSSION

Our results suggest that estimates of southern flying squirrel population structure may be biased if they are based solely on one capture method. For example, both male and female juvenile southern flying squirrels were more likely to be captured from cavities than in Sherman traps, and adult males and females in reproductive condition were more likely to be captured from cavities in one of two years. Further, adult males and females were captured at different rates in traps and cavities in 1994, and this could affect sex ratio estimates. Finally, the number of southern flying squirrels removed from red-cockaded woodpecker cavities may not be a good reflection of the number of squirrels using an area.

Although capturing southern flying squirrels from cavities appears to be more efficient than trapping, one trap-night probably is not equivalent to one cavity inspection because multiple captures in cavities are possible and the overall number of cavity inspections is lower. Nonetheless, capture success for both methods differed between years but in opposite ways. Capture success for traps increased from 1994 to 1995, whereas capture success in cavities decreased. The reasons for the differential trends in capture success are not clear. Although the decline in capture success in cavities may have been due to our removal of squirrels from cavities in 1994, this is not likely. No decline in southern flying squirrel use of red-cockaded woodpecker cavities was observed at the Savannah River Site to the south of CSNWR in Aiken County, South Carolina, after 9 y of continuous removal (Loeb and Ruth, 1995). Other factors, such as differences in the spatial and temporal distribution of food resources, particularly mast; forest management activities in surrounding habitats; or changes in the availability of other nesting sites may have resulted in the year-to-year differences in capture success. Because cavities provide protection from the elements, differences in temperature and precipitation between years could have contributed to differential use of cavities between years. Although average minimum monthly temperatures and rainfall totals were similar between years, rainfall in March 1994 was about 2.5 times greater than rainfall in 1995. The higher rainfall totals, coupled with lower temperatures during that period, may have accounted for some of the higher cavity use in 1994 compared to 1995.

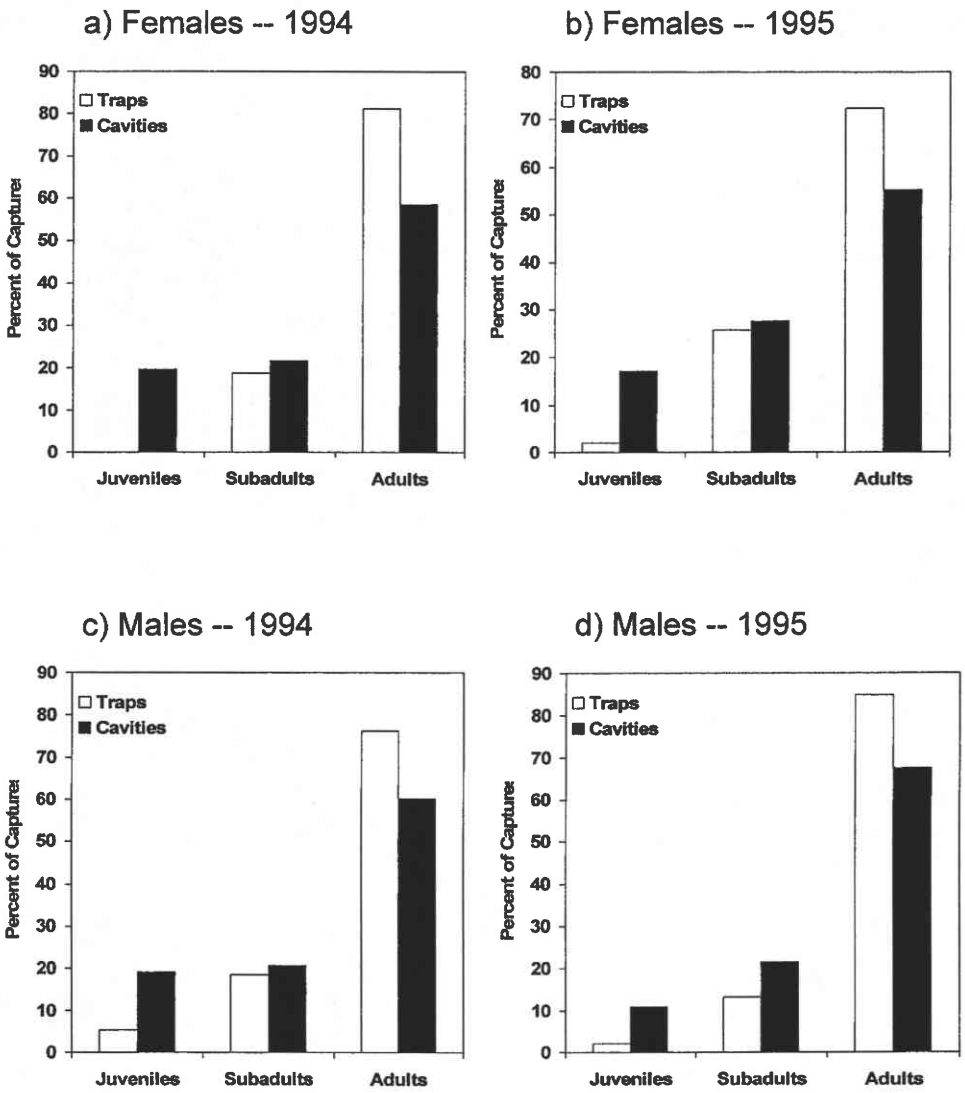

FIG. 1a–d.—Proportion of female and male juvenile, subadult and adult southern flying squirrels (*Glaucomys volans*) captured in traps and in red-cockaded woodpecker (*Picoides borealis*) cavities from March through June, 1994 and 1995 on the Carolina Sandhills National Wildlife Refuge, Chesterfield County, South Carolina

Whatever the factors affecting capture success in cavities and traps, our results suggest that the number of flying squirrels in cavities may not be a true reflection of the number of flying squirrels using an area. These findings are particularly relevant for researchers and managers that are monitoring the effects of habitat management on use of red-cockaded woodpecker cavities by southern flying squirrels (*e.g.*, Conner *et al.*, 1996; Mitchell *et al.*, 2005). Further, our results suggest that the use of only nest boxes to assess the response of southern flying squirrels to forest management may not be sufficient to fully understand southern flying squirrel habitat use.

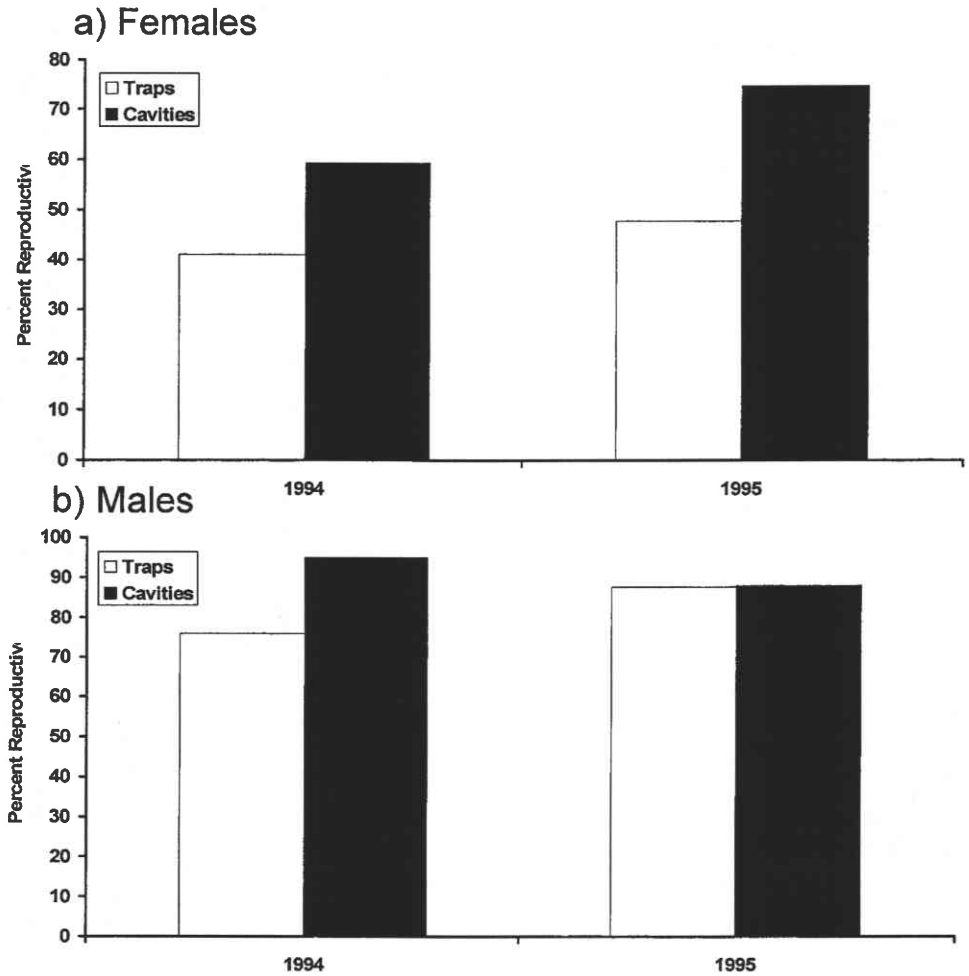

FIG. 2a–b.—Proportion of reproductive adult male and female southern flying squirrels captured in traps and cavities from March through June, 1994 and 1995 on the Carolina Sandhills National Wildlife Refuge, Chesterfield County, South Carolina

The disparity between age structure estimates based on data obtained by different capture methods was primarily due to differences in the number of juveniles captured in cavities and traps. Flying squirrels begin to become independent and start moving outside the nest at approximately 6 wk (Sollberger, 1943; Riter and Vallowe, 1978; Linzey and Linzey, 1979). Therefore, it is not surprising that most of the juveniles we captured were in cavities. Although we did not detect a significant difference in age ratios between capture methods when we only examined the subadult and adult age classes, a greater proportion of subadults were captured in cavities than in traps in both years. In Maryland, mean home ranges of adult male and female southern flying squirrels were 2.45 and 1.95 ha, respectively, whereas home ranges of juveniles averaged 0.61 ha (Bendel and Gates, 1987). Subadult southern flying squirrels are not fully developed physiologically or behaviorally and may be unable to move long distances efficiently (Bendel and Gates, 1987). If movements are restricted, this may decrease the probability that sub-adults will be captured in traps.

Sex ratio estimates based on trapping or nest boxes alone may not represent the true proportions of adult males and females in southern flying squirrel populations. Because our study was conducted during periods of southern flying squirrel reproduction and parental care, the tendency toward intrasexual differences in trappability were probably the result of reproductive condition. Males are polygynous and may increase their home range to increase the probability of encountering mates (Bendel and Gates, 1987; Fridell and Litvaitis, 1991). Greater movement should result in increased capture rates of reproductive males in Sherman traps. However, we observed higher capture rates of reproductive males in red-cockaded woodpecker cavities in 1994. This may have been a result of aggregative behavior of reproductive males in cavities (Layne and Raymond, 1994). Reproduction and subsequent parental care greatly increase energy expenditures of reproductive females (Muul, 1968). Accordingly, conditions associated with pregnancy (*e.g.*, higher energy demands, parental responsibility) may restrict female movement (Bendel and Gates, 1987; Fridell and Litvaitis, 1991), and higher capture rates of reproductive females from cavities in 1995 may have been a result of decreased female movement.

Because it is often difficult to directly measure small mammal reproductive effort and success, indirect measures such as age and sex ratios are commonly used (Lancia *et al.*, 1996). Age and sex ratios are also good indicators of source and sink habitats (Van Horne, 1983). Thus, accurate estimates of these parameters are critical to understanding small mammal population dynamics and the responses of small mammals to changes in habitat. Our results suggest that, when possible, both trapping and nest box or cavity examinations should be done to ensure unbiased estimates of southern flying squirrel population abundance and age and sex structure. When it is not possible to use both methods, caution should be used in making inferences regarding population size and structure.

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