Sciurus niger
Fox Squirrel

Sciurus niger Linnaeus, 1758:64. Type locality probably southern South Carolina (Hall, 1981).
S. cinereus Linnaeus, 1758:64. Type locality, “America Septentrionalis.”
S. vulpinus Gmelin, 1788:147. Type locality, “eastern United States including Blue Mountains” of Pennsylvania.
S. capistratus Bosc, 1802:145. Type locality from “Charleston, South Carolina.”
S. ruhvense Geoffroy St.-Hilaire, 1803:176. Type locality, Mississippi Valley probably between southern Illinois and central Tennessee (Osgood, 1907).
S. ludovicianus Cuvier, 1806:47. Type locality, “Red River of Louisiana.”
S. ruber Rafinesque, 1820:4. Type locality “Missouri Territory.”
S. macroura Say, 1823:115. Type locality, “northeastern Kansas.”
(Not Sciurus macroura Pennant, a species of Rattafa.)
S. texianus Bachman, 1839:86. Type locality, “Mexico.”
S. subauratus Bachman, 1839:87. Type locality, “procured in the markets of New Orleans.”
S. audubonii Bachman, 1839:97. Type locality unknown but probably near New Orleans, Louisiana.
S. rubricaudatus Audubon and Bachman, 1851:30. Type locality, “Kentucky.”
S. sayii Audubon and Bachman, 1851:274. Type locality, somewhere in bottomlands of Wabash, Illinois, or Missouri rivers, or Michigan (Hall, 1981).
S. limitis Baird, 1855:381. Type locality “on Devil’s river, [Valverde Co., Texas].”
Macrocystus neglectus Gray, 1867:425. Type locality “Wilmington, New Castle Co., Delaware.”

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuroidea, Family Sciuridae, Subfamily Sciurinae, Tribe Sciurini, Subtribe Sciurina, Genus Sciurus, Subgenus Sciurus. Twenty-eight species of Sciurus are known (Hoffmann et al., 1993); 10 subspecies of S. niger are recognized (Hall, 1981): S. n. asiaceennis Howell, 1919:37. Type locality “Everglade, Lee County, Florida.”
S. n. bairdianus Lowery and Davis, 1942:156. Type locality “10 mi. NW Enon, Washington Parish, Louisiana.”
S. n. cinereus Linnaeus, 1758, see above. Type locality restricted to “Cambridge, Dorchester County, Maryland” by Barkalow (1956). (Includes neglectus.)
S. n. limitis Baird, 1855, see above.
S. n. ludovicianus Cuvier, 1806, see above. Type locality restricted to Natchitoches Parish by Lowery and Davis, 1942:164. (Includes texianus.)
S. n. niger Linnaeus, 1758, see above. (Includes capistratus.)
S. n. ruhvense Geoffroy St.-Hilaire, 1803, see above. (Includes rufer, macroura, magnicaudatus, rubricaudatus, sayii.)
S. n. shermani Moore, 1956:56. Type locality from “2 miles E. of University of Florida Conservation Reserve, Wealak, Putnam County, Florida.”
S. n. subauratus Bachman, 1839, see above. Type locality restricted to Iberville Parish, Louisiana by Lowery and Davis, 1942:166. (Includes auduboni.)
S. n. vulpinus Gmelin, 1788, see above.

DIAGNOSIS. Sciurus niger lacks an upper P3 unlike sympatric congeners, S. aberti, S. carolinensis, S. griseus, and exotic S. aureogaster in Florida. Where sympatric with S. aberti, S. niger lacks hair tufts on the ears, dorsal pelage is not gray, baculum lacks a keel formed by an expanded distal end and is ca. 16 mm long (Hall, 1981; McGrath 1987). S. carolinensis, the only congener with which geographic overlap is appreciable, is usually 20% smaller in body size, and guard hairs are tipped with white not tan or auburn (Flyer and Gates, 1982). However, S. niger from the eastern United States may have white-tipped guard hairs, but the larger body size of fox squirrels remains evident. Unlike S. griseus, introduced S. niger lacks a gray dorsum, the baculum lacks a distal keel and ventral tuberosity, and the posterior of the jugal is not twisted to reveal the medial surface (Hall, 1981; McGrath, 1987).

GENERAL CHARACTERS. Sciurus niger (Fig. 1) is a medium-sized tree squirrel with no sexual dimorphism in size or color. Ranges of external measurements (in mm) are: total length, 454–698; length of tail, 200–330; length of hind foot, 51–82 (Hall, 1981). Body mass ranges from 507–1,361 g (Flyer and Gates, 1982).

Dorsal pelage is variable; fox squirrels from the western and northern portions of the natural range are grizzled with a suffusion of buff to orange. The venter can be white to cinnamon but usually is russet (Baumgartner, 1943a; Flyer and Gates, 1982). Fox squirrels in the southeastern United States are grizzled gray to agouti to black on the dorsum with white or cream nose, ears, and feet, and a black crown and nape (Kiltie, 1992; Moore, 1956; Weigl et al., 1989). Fox squirrels from the central United States coast are silvery gray and may be washed with buff on the hips, feet, and head; tail is pale gray; underparts are white to pale gray but may be cinnamon (Flyer and Gates, 1982). Melanism is common, especially in the southeastern United States (Kiltie, 1989, 1992). Albinoism is rare (Baumgartner, 1943a; Moore, 1956).

The skull (Fig. 2) is short with broad, expanded zygomatic. The braincase is broad and posteriorly depressed. The rostrum is laterally compressed and narrow; the frontal area is flattened; auditory bullae are moderately inflated. Dental formula is 1/1, c 0/0, p 1/1, m 3/3, total 20 (Flyer and Gates, 1982). Mean cranial measurements of 41 specimens from Arkansas, Florida, Kansas, Louisiana, Maryland, and Mexico (in mm) are: greatest length of skull, 66.2; zygomatic breadth, 37.8; palatal length, 29.9; diastema length, 16.0; least interorbital breadth, 20.3; nasal length, 24.2; length of maxillary toothrow, 12.0 (McGrath, 1987).

DISTRIBUTION. Sciurus niger is found in much of the eastern and central United States extending northward into the

Fig. 1. Sciurus niger from Eugene, Lane Co., Oregon.
in July or August (Flyer and Gates, 1982). Lactating females molt after young are weaned (Baumgartner, 1943a). The molt into adult pelage occurs at 75-90 days of age (Moore, 1957). During winter, ears are heavily furred with pale colored hair (Flyer and Gates, 1982); the foot sole becomes densely haired (Pocock, 1923). Mystacina are longer after allowing for body size than those of ground-dwelling sciurids (1:71:1 ratio of vibrissal length: head width; Ahl, 1987).

The eight mammae (four pectoral, two abdominal, and one inguinal) become black in the first pregnancy and generally retain this coloration (Flyer and Gates, 1982). Ten mammae were reported (Svihla, 1931).

Inferior incisors become indeterminate; molariform cheekteeth exhibit brachyodont and bunodont structure (Flyer and Gates, 1982). Upper incisors are opisthodont; the mean inciso-rostral angle is 76.1° with incisors covering an arc of 208° (Landry, 1957).

The stance is plantigrade (Gurnell, 1987). Anatomical adaptations for climbing and jumping include: sharp recurved claws, elongated digits and limbs, well-developed extensors of数字化的肌肉, trapezius group muscles, clavicles, and abdominal musculature. The first digit is reduced on the front feet. In Kansas specimens, the average lengths of the other digits (in mm) are: 35, 40, 43; carpals are pisiform and average 4 mm. There are an average of 25 caudal, 3 (or 4) sacral, 7 lumbar, 12 thoracic vertebrae, and 12 thoracic ribs (Petelska, 1986). An adult female with a fifth leg attached by soft tissue at the inguinal area has been described (Bowers and Kirkland, 1968).

Climatic variation in reverse of Bergmann’s Rule exists in body size east of the Appalachians; body size is smallest in the north. Fox squirrels to the west follow the pattern predicted by Bergmann’s Rule (Weigl et al., 1989). An east-westcline also exists, with the smallest fox squirrels in the west (Purduel, 1980).

Heart rate ranges from 150 to 450 beats/min; fear tachycardia occurs in free-ranging animals in response to stimuli (Smith and Johnson, 1984). Mean hematological characteristics are hematocrit = 38%, red blood cell count = 7.33 x 10^6 cells/mm^3, and mean corpuscular volume = 52 μm^3 (Dunaway and Lewis, 1965). Mean rectal temperature is 40.6°C (Havera, 1979a). The tail possesses a counter-current system of vascular bundles at the base; the tail’s insulative value increases 17.2% to 0.035°C kcal·h·°C·m·m^2·day when the tail is raised above the body while providing shade and slowing heat gain (Mucholinski and Shump, 1979).

Energy assimilation rates range from 388 to 578 kJ/squirrel/day. Food consumption peaks in spring or autumn with a voluntary decrease in winter (Knee, 1983). Fox squirrels fed lab show consumed 49.3 g/day in May, 46.1 g/day in October, and only 18.3 g/day in February (Havera, 1989a). Juveniles consume 50% more food per unit of metabolic weight (body mass^0.75) than adults (Short and Duke, 1971). Energy requirements for maintenance in autumn...
are 162 kcal day⁻¹ kg⁻¹ of body mass (Husband, 1976). Urinary loss of energy is 0.6–0.7% and digestive efficiencies range from 80% on a lab diet of 90% to 96% on a black walnut (Juglans nigra) diet; these diets follow food consumption patterns. Females produce 2 litters/year (Harnishfeger, 1978) but this percentage may be higher in some populations (Allen, 1942). Reproduction may be tightly linked with food availability (Nixon and McClain, 1969). Prevalence of lactation fell from 88 to 0% after a poor food crop (Weigl et al., 1989).

The baculum is 12–14 mm long in S. n. rufuswegi and 13.3 mm long in S. n. niger (Long and Frank, 1968; Wade and Gilbert, 1942). Males reach sexual maturity as early as 10–11 months (Kirkpatrick, 1955) and undergo an irregular cycle of testicular development; functional testes are present in the scrotum. Two annual peaks in male reproductive activity occur in November–February and May–July; however, functional males are found in all months (Brown and Yeager, 1945; Kirkpatrick, 1955; Weigl et al., 1989). A period of male sexual quiescence characterized by regressed testes, degenerated glands, and apparent cessation of spermatogenesis usually occurs August–October (Kirkpatrick, 1955; Mossman et al., 1955). Active testes averaged 6.9 g, but inactive testes were 0.4 g (Kirkpatrick, 1955). The prostate gland is an elongated ovoid, Cowper’s glands are paired and spherical, seminal vesicles are paired and prismatic in shape, and the single bulbular gland is three-lobed and conical in shape (Kirkpatrick, 1955; Mossman et al., 1955).

Epiphysial spermatoozoa aggregate into cylindrical bodies then separate becoming single or a rouleaux (Marten et al., 1970). Neonates are naked except for vibrissae, weigh 13–18 g, and are 50–60 mm long. Claws are well developed. The dorsum darkens after 7–10 days as hair emerges. By 3 weeks of age, downy hair begins to fill the dorsum of the tail, the ears open, and the lower incisors erupt. Eyes open, upper incisors erupt, and hair appears on the ventral tail surface in week 5. Weaning begins at 8 weeks and is not complete until at least 12 weeks of age (Allen, 1942). The instantaneous positive growth rate is highest during the first week of life (87% of birth mass) and gradually declines to 8% at weaning; body mass at 1 year of age averages 92% of maximum body mass (Nixon et al., 1991).

ECOLOGY. Although found in a diversity of deciduous and mixed-forest habitats, fox squirrels are common in forest patches <40 ha with an open understory (Nixon and Hansen, 1987). Low understory stem densities are an important component in some localities (Taylor, 1974) but not in others (Brown and Batzli, 1984). Densities of S. niger are higher in habitats composed of trees that produce winter-storable food such as oaks (Quercus), hickories (Carya), walnuts (Juglans), and pines (Pinus; Nixon and Hansen, 1987; Weigl et al., 1989). Due to annual variability in mast production, a diversity of tree species is important to support high densities of fox squirrels (Nixon and Hansen, 1987).

Western range extensions are associated with riverine corridors of cottonwoods (Populus deltoides; Knapp and Swenson, 1986) and fencerows of osage orange (Maclura pomifera; Packard, 1956). In Colorado, fox squirrels inhabit mixed conifer-deciduous forests (Littledale, 1984). In Florida, S. n. aureoviridis is restricted to diminishing stands of cypress (Taxodium distichum), slash pine (Pinus elliottii) savanna, and mangrove (Avicennia germinans) swamps (Williams and Humphrey, 1979). Populations of S. n. limitis and S. n. ludovicianus in Texas are found primarily in upland pine–oak–hickory woodlands (Goddred, 1937; Lowery and Davis, 1942). Endangered S. n. cinerus is found in savanna of mature hardwoods and loblolly pine (P. taeda; Taylor, 1974). In North Carolina, S. n. niger frequents open mature pine–oak, especially longleaf pine (P. palustris) and turkey oak (Q. laevis; Weigl et al., 1989). S. n. shermani in Florida prefers longleaf pine savanna and edges of live oak forests (Q. virginiana; Kantola and Humphrey, 1990). The rapid loss of preferred habitats is likely responsible for the precarious conservation status of four subspecies: S. n. aureoviridis, S. n. cinerus, S. n. niger, S. n. shermani.

Because of dry conditions, female S. n. aureoviridis require 8–30 years depending on wood type (Baumgartner, 1939a). Addition of artificial nest boxes did not increase densities or survival except for adult males (Nixon et al., 1984). However, 1–2 boxes/2.5 ha may be beneficial (Nixon and Hansen, 1987). Girdling or otherwise degrading of hardwoods can detrimentally affect McGlasson et al. (1967). Selective cutting of trees ≥0.5 cm without removal of culled trees has little effect on population parameters except for temporarily low recovery rates of females after 40–40% of the merchantable volume.
was removed (Nixon et al., 1980). Winter feeding with corn did not increase survival or densities (Havera and Nixon, 1980).

Brown rats (Rattus norvegicus) in woodlots and second growth in the southeastern United States are 1.0–3.5/ha (Baumgartner, 1943b; Nixon and Hansen, 1987) but reach 12 squirrels/ha (Koprowski, 1985). However, densities in the southeastern United States are 0.12 squirrels/ha (Kantola and Humphrey, 1990) and 0.04 squirrels/ha (Moore, 1957) for S. n. shermani and 0.03 squirrels/ha for S. n. niger (Weigl et al., 1989). Food can be limiting during winter when autumn nut crops may be exhausted prior to spring flowering of trees and late spring-early summer when fruits may be depleted prior to ripening of nut crops. After frost damages developing tree seeds, body mass, survival, and reproduction decrease (Koprowski, 1991c; Nixon and McClain, 1969).

Sex ratios (male: female) vary from 0.88–1.05/1 in nestlings (Brown and Yeager, 1945; Weigl et al., 1989), 0.82–1.3/1 in juveniles, and 1.10–1.14/1 in adults (Nixon et al., 1975; Weigl et al., 1989) but do not differ from a 1:1 sex ratio. Annual trends in age structure reflect seasonal reproduction with adults composing 83% of the population in April prior to emergence of spring litters and only 30% in October when juveniles from both spring and summer litters remain in the population (Brown and Yeager, 1945). A declining population consisted of a few old adults (Nixon and McClain, 1969). Immature animals compose 13–81% of populations (Brown and Yeager, 1945; Nixon et al., 1975).

Durations of residence were 4.7 months for juveniles, 13.5 months for subadults, 27.4 months for yearlings, and 25.7 months for adults. Residence times were evidenced by recaptures of the same animals. Annual adult survivorship is generally >60% with mean annual mortality estimated as 34% for males and 37% for females (Hansen et al., 1986). Dispersal peaks in autumn when most subadults move; however, this autumn-shuffling may include many adults (Allen, 1973; Baumgartner, 1943b, 1948; Koprowski, 1985). Mass migrations are rare, but small scale migrations are observed occasionally (Schuger, 1949). Turner’s migration (99.1% of the population) were 11.7 years for unattended populations (Hansen et al., 1986) but <3.5 years for hunted populations. Populations can sustain a hunting loss of <50%, but only immigration sustained a population with a 50% population loss (Nixon et al., 1974, 1975). Maximum longevity is 12.6 years for females and 8.3 years for males (Koprowski et al., 1988); a captive female survived 13 years (Flyger and Gates, 1982). Weather and survival are not correlated (Hansen et al., 1986). Only extremes in seed crops likely affect adult survival (Hansen et al., 1986; Nixon and McClain, 1969; Nixon et al., 1975), although juvenile survival is influenced particularly by seed crops (Koprowski, 1991a). Supplemental feeding with corn did not increase survival (Havera and Nixon, 1980); however, supplements of natural mast may increase survival (Brown and Yeager, 1985c).

Predators of fox squirrels include timber rattlesnakes (Crotalus horridus), black rat (Elaphe obsoleta) and pine (Pineus melanoleucus) snakes, goshawks (Accipiter gentilis), red-tailed (Buteo jamaicensis), red-shouldered (B. lineatus), rough-legged (B. lagopus), ferruginous rough-legged (B. regalis) hawks, and great horned owls (Bubo virginianus). Mammalian predators include opossums (Didelphis virginiana), weasels (Mustela frenata), raccoons (Procyon lotor), red fox (Vulpes vulpes), gray fox (Urocyon cinereoargenteus), bobcats (Felis rufus), wolves (Canis lupus), coyotes (C. latrans), dogs, and cats (Flyger and Gates, 1982; Packard, 1956; Weigl et al., 1989).

Pesticides levels in trees are low; however, 11% of assayed squirrels from Illinois contained dieledrin (mean = 0.0011 ppm) and 89% contained DDE (mean = 0.0041 ppm; Havera and Duzan, 1977). Normal porphyria characterized fox squirrels and resembles congenital erythropoietic porphyria in humans. Porphyria metabolism is defective and uroporphyrin I accumulates in teeth, bones, and tissues. As a result, bones are pink; bones, thin sphenoid tissue sections, and urine fluorescent bright red under ultraviolet light. Fox squirrels do not display skin lesions or hemolytic anemia and can serve as a useful model for medical research (Flyger and Levin, 1977). California encephalitis virus and western equine virus are known from fox squirrels (Flyger and Gates, 1982). Rabies is rare (Capucci et al., 1972). Francisella tularensis (tularemia). Yersinia pestis (plague), Mycobacterium tuberculosis, and Leptospira canicola were isolated from Florida (Florida) in Florida have been reported (Flyger and Gates, 1982). Coccidioides-related deaths were reported in Iowa (Mockesley and Vohs, 1971).

Larvae of bot flies (Ctenocephalides canis) parasitize squirrels in autumn when the subcutaneous myiasis infest 5% of animals in Mississippi (Jacobson et al., 1979, 1981). Infestations of mange mites (Sarcoptes scabiei) and Cheyletus (Cheyletus) may result in death (Kazacos et al., 1983; Flyger and Gates, 1982). Flyger and Gates (1982) provide an extensive list of parasites from which the following list was compiled unless otherwise noted. Protoposa —Eimeria ascen- tensis, E. confusa (Joseph, 1973), E. kniplingi, E. lanceenteronis, E. ontarioensis (Joseph, 1973), Gestoda—Bostricosphecus scutari, Choenotornia sciarica, Cellinemiia bifurcata, Cysticerus passiflorum, Hymenolepis diminuta, Mesocestodes latus, Multiceps serialis, Raillietinea bakeri, Taenia hydatigena, T. mustelae (Langham et al., 1990), T. pisiformis, T. taenioformis; Acanthocephala —Moniliformis clarki; Nematomorpha —Acanthostomas柱状or, A. lumbricoides, Bowmahil wilsoni, Capillaria hepatica, Enterobius vermicularis, Heliocondrema Hassall, Macracanthorhynchus hirudinaceus, Physaloptera massoni, Strongyloides robustus, Trichinella spiralis; Acantho—Amblyomma americanum, A. maculatum, A. vul- culatum, Arachnolepis glaucomlaria, A. megavalentris, Derma-centar variabilis, Eulaeolaelaps stabularis (Moore, 1957), Euertobiurca alfredalus, Haemaphysalis leporispalustris, Haemolaelaps megavalentris, Ixodes cocoee, I. heartiei, I. scapularis (Moore, 1957), Notodurus douglasi (Kazacos et al., 1983), Sarcoptes scabiei, Trom- bicula alfredalus (Moore, 1957), T. whitoni (Moore, 1957), Anopluropsa—Enderleinellus longiceps, Hoplopleura sciarica, Neo- haematopus scutarius; Siphonaptera—Ceratophyllus fasciatus, Ctenocephalides felis, Echinophaga gallinaeae, Hoploparys affinis, Leptopsylla segnis, Opiloides robustus, Orchope- dos hoardi, Scutulus.
MAMMALIAN SPECIES 479

ylius americana), pawpaw (Asimina triloba), persimmon (Diospyros), blue gum (Eucalyptus globulus), Russian olive (Elaeagnus angustifolia), coffee tree (Triumfetta diversifolia), locust (Gleditsia triacanthos), tulip tree (Liriodendron tulipifera), hop hornbeam (Ostrya virginiana), cottonwood, and willow (Salix).

Seed and catkins of gymnosperms are also eaten, including cedar (Juniperus), cypress (Taxodium distichum), and pines (especially longleaf pine and pond pine, P. serotina, in the southeastern United States; Packard, 1956; Weigl et al., 1989). Herbaceous species eaten include grasses, sedges, grape (Vitis), cocklebur (Xanthium), greenbrier (Smilax), huckleberry (Gaylussacia), blueberry (Vaccinium), bitternut (Carya cordiformis), and blackberry (Rubus; Baumgartner, 1939b; Korschgen, 1985; Nixon et al., 1986). The sugary pith of yellow buckeye (A. octandra) is eaten (Havera et al., 1976) and bark is occasionally ingested (Packard, 1956). Corn, oats, sorghum, soybeans, and wheat are eaten especially in winter; fruits of apple, cherry, blueberries, and oranges are also eaten (Baumgartner, 1939b; Korschgen, 1981; Wolf and Roest, 1971). Gravel and soil are ingested by females in winter and spring; fungi are consumed primarily in summer and winter (Korschgen, 1981; Weigl et al., 1989). A preference for salt (primarily sodium) occurs in spring as potassium uptake rises and again in autumn in association with low salt concentrations of juices (Weigl et al., 1989).

Animal foods are usually ingested in trace amounts including gall insects (Pemphigus, sp., Pachysylla mamba), various species of moths, butterflies and caterpillars (Lepidoptera), grasshoppers (Acrididae), walkingsticks (Phasmatidae), may-beetles (Scarabaeidae), cicada flies (Cicadidae), weevils (Curculionidae), ants (Formicidae), and flies (Diptera; Baumgartner, 1939b; Korschgen, 1981; Packard, 1956). Other animal foods include birds and bird eggs (Packard, 1956; Shaffer and Baker, 1991) and dead fish (Fairbanks and Kropowski, 1992). Camouflage has been reported (Allen, 1943). Fox squirrels are omnivorous; 80% of diet is on local scale (Curnell, 1987). Historically, corn crops of Native Americans and early colonists suffered high depredation (Schorgar, 1949). Pecans, English walnuts, avocados, oranges, and strawberries are eaten but losses are not excessive (Flyer and Gates, 1982; Wolf and Roest, 1971). The oak wilt fungus is transmitted by fox squirrels under experimental conditions (Himelick and Curl, 1955). Fox squirrels can be a nuisance by raiding gardens and bird feeders. Live-trapping with release of squirrels >10 km away may effectively deal with problem individuals (Flyer and Gates, 1982). State or provincial wildlife agencies must be contacted prior to trapping this game animal. Fox squirrels may be repelled from holes in wooden walls and roof shingles by using paradichlorobenzene or napthalene (moth balls or crystals). Gnawing of plant stumps or tree bark may be reduced with the application of tetramethriniluradisulfide. Methylene monyl ketone crystals and paradichlorobenzene are used to repel animals from lawns, gardens, and property borders, but have limited effectiveness (Jackson, 1983). Fox squirrel use of electrical power equipment as pathways can result in power outages (Hamilton et al., 1989).

Economic value is primarily from hunting and travel-related revenues. Historically, squirrels were a quality food to Native Americans and the early European colonists (Schorgar, 1949). The nonconsumptive value of tree squirrels is also great; collectively, squirrels rank second to songbirds in value to nature watchers and photographers (Shaw and Mangun, 1984). Additionally, fox squirrels are excellent subjects for education on various problems in behavior and ecology (Brown and Drownhower, 1987). By burying forest nuts in open grasslands, fox squirrels are instrumental in succession of grasslands to forests (Stapanian and Smith, 1986).

Fox squirrels can be live-trapped with box traps baited with peanut butter, corn, sunflower seeds, or nuts and placed near large trees; prebaiting for several days may increase trap success (Baumgartner, 1940; Brown and Batli, 1965a). Traps should be checked twice daily to prevent mortality. Success is greatest in winter and spring (Kropowski, 1983). Squirrels are safely handled in a wire mesh or cloth handling cone to restrict movement (Baumgartner, 1940; Weigl et al., 1989). Squirrels are temporarily marked for observation with fur dyes (Berdard, 1972). Semi-permanent identification is accomplished with ear tags (Baumgartner, 1940), or, if field observations are desired, by ear tags equipped with streamers (Kropowski, 1988). Permanent identification is possible by toe-clipping (Baumgartner, 1940) or, if field observations are desired, by toe-clipping (Baumgartner, 1940) or, if field observations are desired, by freeze branding (Hadov, 1972) or freeze marking (Kropowski, 1991a). Time-area counts may be useful to estimate squirrel abundance but are labor-intensive and must be conducted during peak periods of activity (Bouffard, 1982). Some mark-recapture methods especially in high density populations of trappable squirrels are useful (Baumgartner, 1939b; Kropowski and Bafranchuk, 1983; Kropowski, 1984). Fox squirrels in the southeastern United States are difficult to trap; checking nest boxes at night is the most successful method of capture (Weigl et al., 1989).

Fox squirrel nestlings can be raised on milk followed by bread and milk and finally by fruits and vegetables as young mature (Crandle, 1964). Adults can be maintained on a diet composed of a variety of nuts, seeds, fruit, lab chow, and a vitamin supplement; large (>2 by 2 by 4 m) outdoor pens with nest boxes are most successful (Weigl et al., 1989).

BEHAVIOR. Diet activity is bimodal in spring–fall peaking at 2 h after sunrise and 2–4 h before sunset; a unimodal pattern occurs in winter with a midday peak at 1000–1400 h (Adams, 1984; Geeslin, 1970; Hicks, 1949; Hilliard, 1979). In summer, an additional peak in activity may also occur from 1100–1200 h (Hicks, 1949). Greatest activity in winter is during early morning, possibly related to breeding activity (Packard, 1956). Activity is diurnal but may begin just before sunrise or continue shortly after sunset (Geeslin, 1970). Weather has a negligible impact on activity; however, high winds (>14.5 km/h) result in low activity (Hicks, 1949). McCloskey (1975) details the ontogeny of behavior from kin to adulthood. Sleeping and crawling dominate the repertoire of nestlings until 21 days of age when they begin to walk. At day 31, nestlings groom and move their tails. Juveniles can run and jump at 37 days of age. Independent feeding and drinking begin about day 45 and caching was first observed day 65.

Average home ranges vary from 0.85 to 17.2 ha for females and from 1.54 to 42.8 ha for males; the largest home ranges are reported in the southeastern United States (Adams, 1976; Benson, 1962; Geeslin, 1970; Kats and Kemp, 1960; Weigl et al., 1989). Home range overlap is extensive and territories are not well defined (Allen, 1943; Benson, 1980). Adults, especially females, may defend exclusive core areas thereby limiting immigration (Havera and Nixon, 1978; Kats and Kemp, 1960; Weigl et al., 1989). Adult females are important in regulating densities. Ingress of juveniles and subadults of both sexes and adult females was higher on grids from which adult females were removed than on control grids or grids from which males were removed (Hansen et al., 1986). Furthermore, immigrant survival is negatively correlated with the number of resident adults, especially adult females (Hansen et al., 1986).

All juveniles probably disperse from their natal areas (Hansen et al., 1986; Kropowski, 1991b) although some may nest with their mother through a winter (Adams, 1984; Allen, 1943). Agonistic interactions peak during periods of heightened reproductive activity (Havera and Nixon, 1980) and aggression may be instrumental in natal dispersal (Adams, 1984). The longest dispersal movement reported is 64.4 km (Allen, 1943).

Sex and age are the primary determinants of dominance; males dominate females and adult males dominate juveniles (Benson, 1980; Bernard, 1972). Threat is characterized by an upright stance with tail over the back and may be preceded or followed by a tail flick and rapid approach by the aggressor. Submissive animals usually retreat (McCloskey, 1975). Gregarious nesting is rare with <5% of nests occupied by >1 squirrel (Christensen, 1985; Kropowski, 1991b). Adult male groups during winter and adult male–female pairs during breeding seasons are the most common associations (Adams, 1984; Kropowski, 1991b; Nixon et al., 1984; Weigl et al., 1989). Juveniles and adult males aggregate more than adult females when outside of dens (Armitage and Harris, 1982).

Tail movements such as rapid fore-and-aft jerking are used to reduce aggression or signal an aggressor’s intentions. The variable response of fox squirrels to tail movements suggests that more subtle visual signals are used (McCloskey, 1975; McCloskey and Shaw, 1977).

Traditional scent marking points are found in protected sites on trees and are visited regularly by male fox squirrels (Kropowski, 1993b), which deposit scent from glands in the oral–labial region (Benson, 1980). Females visit these points but rarely mark (Kropowski, 1993b). Both sexes mark substrate at non-traditional, dispersive sites while traversing their home ranges; dominant animals mark most often (Benson, 1980).

The most common vocalization by fox squirrels is a series of barks. A chatter bark is given after being startled. Tooth chatter
and breathy barks are indicative of restlessness and mild stress. Low frequency groans are emitted by restrained squirrels. Grunts and longer-lasting calls are given by unrestrained animals and during male-male barks. A scream consisting of two parts is produced by distressed squirrels. A high pitched whoosh is given during mating

chases (Zelley, 1971).

Fox squirrels swim by a dog-paddle with head, dorsum, and tail above the surface (Applegate and McCord, 1974). Squirrels can run 24.2 km/h at a gallop (Moore, 1957). Most feeding is accomplished in a bipedal stance with items manipulated in the forepaws. Vigilance is accomplished by a bipedal stance with varying degrees of eeriness. Fox squirrels are adept climbers and frequently hang by the hindlimbs and forage with the forelimbs when feeding among tree limbs; climbing is accomplished in a trot or gallop.

Fox squirrels are classic scatterhoarders that disperse food caches. Nuts are carried in the jaws, a hole is dug with the forepaws, and the nut is buried below (<2 cm) the soil surface or covered with leaf litter (Cahalane, 1942). Between 35% and 99% of cached seeds are recovered (Cahalane, 1942; Stapanian and Smith, 1984). Offact is likely important in locating buried nuts. Accuracy in locating buried nuts decreases in dry, sandy substrates, possibly due to poor diffusion of chemical cues (Cahalane, 1942). Acorns with high lipid content are preferred, especially white oaks (Smith and Folmer, 1972). Red oak and black oak acorns were preferred over white oak acorns with a demonstrated preference for acorns of low

tannin content (Ofcarrick et al., 1973); however, diets consisting solely of red oak or black oak acorns were the only nut diets to lead to loss of body mass (Baumgras, 1944; Havera and Smith, 1979). Food choices suggest squirrels forage to maximize energy gain (Smith and Folmer, 1972). Survival of buried nuts decreases with increased food content of the nut and density of nuts in the patch (Stapanian and Smith, 1984). Fox squirrels scatter caches in mutually exclusive areas at densities that minimize loss rates to seed competitors (Stapanian and Smith, 1978). Foraging strategies of free-ranging fox squirrels are complex and change between sites; patch choice is related to the highest short- and long-term rates of energy gain (Steele and Weigl, 1992).

GENETICS. The diploid number of chromosomes for S. n. rufiventris is 40; the fundamental number is 76. The X chromosome is a submetacentric and the Y chromosome is an acrocentric; autosomes consist of 14 metacentrics and 24 submetacentrics (Nadler and Sutton, 1967). Electrophoretic variation was detected at 18 of the 35 loci assayed including acid phosphatase, adenosine deaminase, creatine kinase, fumarase, glucose-6-phosphate dehydrogenase, iso-citrate dehydrogenase, malate dehydrogenase, malic enzyme, mannose-phosphate isomerase, nuclease phospholyase, octanal dehydrogenase, peptidase, 6-phosphogluconate dehydrogenase, phosphoglucomutase, and phosphoglucose isomerase (Moncrief, 1993).

Although fox squirrels occasionally follow female eastern gray squirrels in estrus, copulation is not attempted (Koprowski, 1991; Moore, 1968). Hybridization with conegers is not known (Gurnell, 1987).

REMARKS. Sciurus is derived from the ancient Greek, skia meaning shadow or shade, and oura or tail. niger refers to the black coloration or the type specimen. Additional names are cat squirrel and stump-eared squirrel (Fryer and Gates, 1982).

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LITERATURE CITED


MAMMALIAN SPECIES 479


KOPROWSKI, J. L. 1985. Fox squirrel population trends and reg-


Say, T. 1825. Account of an expedition from Pittsburgh to the Rocky Mountains, performed in the years 1819 and '20, by order of the Hon. J. C. Calhoun, Sec'y of War: under the command of Major Stephen H. Long from the notes of Major Long, Mr. T. Say, and other gentlemen of the exploring party. Compiled by E. James. Vol. 1, Carey and Lea, Philadelphia, 503 pp.


Sexton, O. J. 1990. Replacement of fox squirrels by gray squirrels


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