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Sciurus carolinensis.

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Sciurus carolinensis Gmelin, 1788

Eastern Gray Squirrel

Sciurus carolinensis Gmelin, 1788:148. Type locality "Carolina."
Sciurus Pennsylvanica Ord *in* Guthrie, 1815:292. Type locality "Pennsylvania W of Alleghany Ridge."
Sciurus hiemalis Ord *in* Guthrie, 1815:292. Type locality "near Little Egg Harbor, [Ocean Co.], New Jersey."
Sciurus leucotis Gapper, 1830:206. Type locality "region between York (Toronto) and Lake Simcoe, Ontario."
Sciurus fuliginosus Bachman, 1839:97. Type locality "obtained at New Orleans."
Sciurus migratorius Audubon and Bachman, 1849:265. Renaming of *leucotis*.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Sciuridae, Subfamily Sciurinae, Tribe Sciurini, Subtribe Sciurina, Genus *Sciurus*, Subgenus *Sciurus*. Five subspecies of *S. carolinensis* are recognized (Hall, 1981):

S. c. carolinensis Gmelin, 1788:148, see above.
S. c. extimus Bangs, 1896:158. Type locality "Miami, Dade Co., Florida" (*matecumbei* Bailey is a synonym).
S. c. fuliginosus Bachman, 1839, see above.
S. c. hypophaeus Merriam, 1886:351. Type locality "Elk River, Sherburne Co., Minnesota."
S. c. pennsylvanicus Ord *in* Guthrie, 1815:292, see above (*hiemalis*, *leucotis*, and *migratorius* are synonyms).

DIAGNOSIS. The only naturally sympatric congener, *S. niger*, is >20% larger in body size, lacks a peg-like P3, has a sphenopalatine foramen larger than the optic foramen, and the distance between the upper cheek teeth progressively increases from P4 to M3 (McGrath, 1987). Guard hairs of *S. carolinensis* are tipped with white, not tawny, brown, or orange; tail guard hairs of *S. niger* from the east may be white-tipped but body size differences remain (Flyger and Gates, 1982). *S. carolinensis* lack distinctive hair tufts on the ears, dorsal pelage is gray, and the maxillary plate notch is opposite M1 not P4. The sphenopalatine foramen < optic foramen, distinguishing introduced *S. carolinensis* populations in Europe from *S. vulgaris*. In comparison with *S. griseus*, *S. carolinensis* is smaller (total length < 500 mm), sphenopalatine foramen < optic foramen, baculum lacks a distal keel and ventrally located tuberosity, and the medial surface of the jugal is not visible from above (Hall, 1981; McGrath, 1987).

GENERAL CHARACTERS. *Sciurus carolinensis* (Fig. 1) is a medium-sized tree squirrel with no sexual dimorphism in size or coloration. Ranges of external measurements (in mm) are: total length, 380–525; length of tail, 150–250; length of hind foot, 54–76; length of ear, 25–33. Adult body mass ranges from 300 to 710 g (Barkalow and Shorten, 1973; Hall, 1981).

The dorsum is grizzled dark to pale gray and may be washed with cinnamon on hips, feet, and head. Ears are buff to gray to white in the north; tail is white to pale gray. Underparts are white to gray to buff to cinnamon (Flyger and Gates, 1982). Melanism is common in the north (Innes and Lavigne, 1979) and albinism is rare, although white animals are found in Olney, Illinois, and Marionville, Missouri.

The skull (Fig. 2) is relatively short with broad and expanded zygomata. The braincase is broad and posteriorly depressed. The rostrum is laterally compressed; the frontal area is flattened. Auditory bullae are moderately inflated. The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22; P3 is small and peg-like (Hench et al., 1984). Average cranial measurements (mm) for 32 specimens from Arkansas, Iowa, Kansas, and North Carolina are (McGrath, 1987): greatest length of skull, 60.7; zygomatic breadth, 34.5; palatal length, 27.9; length of diastema, 14.4; least interorbital breadth, 17.9; length of nasal, 20.6; cranial height in vault of skull, 28.4; length of maxillary tooth row, 10.9.

DISTRIBUTION. *S. carolinensis* is found in the eastern United States (U.S.); the range extends west to the edge of the deciduous forest and north to Canada (Fig. 3). Introductions occurred in California, Montana, Oregon, and Washington in the U.S., and Quebec, New Brunswick, British Columbia, Manitoba, Nova Scotia, Ontario, (Barkalow and Shorten, 1973; Flyger and Gates, 1982), and Saskatchewan (Nero, 1958) in Canada. Eastern gray squirrels were introduced to Italy and England from the U.S., to Scotland from Canada (Currado et al., 1984; Lloyd, 1983; Staines, 1986), and to South Africa (Millar, 1980) and Ireland (Lloyd, 1983) from England. An 1880s introduction from England to Australia failed by 1973 (Seebeck, 1984).

FOSSIL RECORD. *S. carolinensis* occurs in 20 North American Pleistocene faunas as early as the late Irvingtonian (Coleman IIA) in Florida (Kurten and Anderson, 1980). Body size increased in the early to middle Holocene and then decreased to present size (Purdue, 1980).

FORM AND FUNCTION. The spring molt begins in March on the head and progresses posteriorly; the autumn molt begins in September on the flanks and proceeds anteriorly. The annual tail molt begins in July (Flyger and Gates, 1982) and proceeds from the distal end (Brown and Yeager, 1945). Lactating females molt after young are weaned (Flyger and Gates, 1982). During northern winters, ears are heavily furred with pale dorsal hair (Flyger and Gates, 1982) and the foot sole becomes densely haired (Pocock, 1923). Mystacial vibrissae are relatively longer (1.69, vibrissal length/head width) than those of terrestrial sciurids (1.01; Ahl, 1987).

The eight mammae (four pectoral, two abdominal, two inguinal) become black with first pregnancy (Flyger and Gates, 1982). The composition of milk is: 60–75% water, 12–25% fat, 7–9% protein,

FIG. 1. *Sciurus carolinensis* from Lawrence, Douglas Co., Kansas.

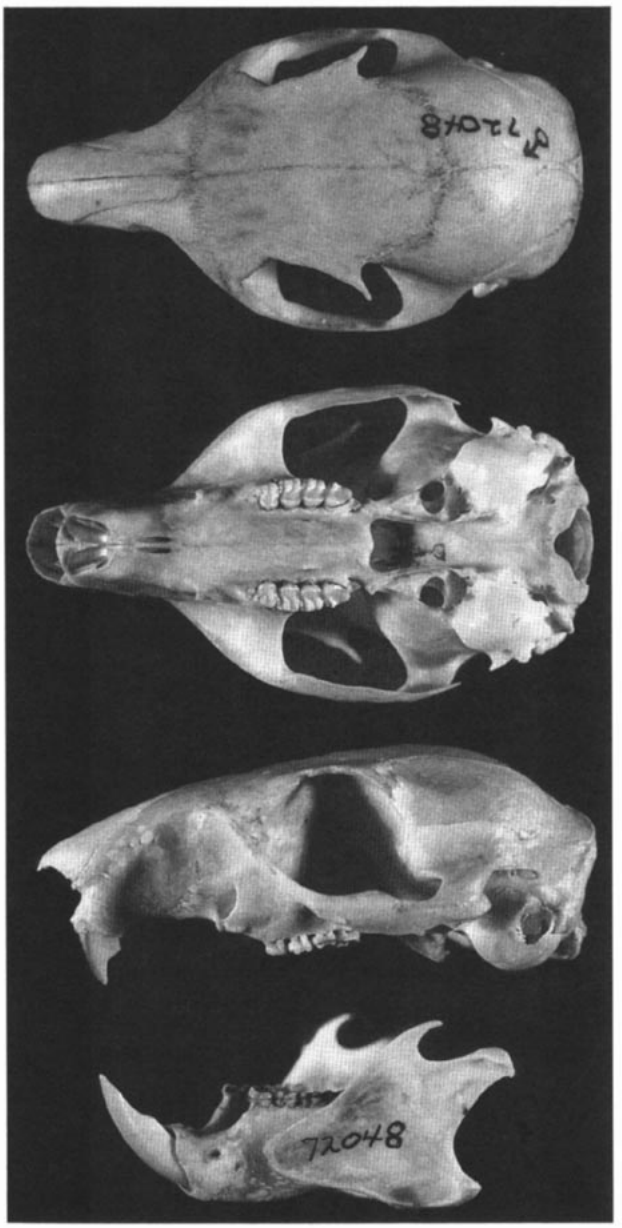

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Sciurus carolinensis* (male from near Barada, Richardson Co., Nebraska, University of Kansas Museum of Natural History 72048). Greatest length of cranium is 62.0 mm. Photographs by S. Hagen.

3–4% lactose, and <1% calcium and phosphorus (Nixon and Harper, 1972).

Incisor growth is indeterminant; molariform cheekteeth exhibit brachyodont and bunodont structure (Flyger and Gates, 1982). A broad, opaque cementum layer is deposited on the roots in summer followed by a thin, dark-staining layer in winter (Hefner, 1971).

Most *S. carolinensis* have 7 sternebrae and 26 presacral vertebrae (7 cervical, 12 rib-bearing thoracic, 7 lumbar) with 3 sacral and 26–29 caudal vertebrae (Thorington, 1972). The hind foot can be reversed by 180° from forward by unusual flexibility in crurotalar, transverse talar and subtalar joint to permit head first descent (Jenkins and McClearn, 1984). Seven toes/foot were reported (Dunaway, 1969). Inner ear ossicles of females are longer than males (Daniel and Roberson, 1987).

Body mass is greatest in the north and smallest in the south (Havera and Nixon, 1978; Uhlig, 1955). Bones of the cranium also follow a north-south cline in size, but size of mandibles and toothrows is conservative possibly due to stabilizing selection on characters involved in mastication (Barnett, 1977; Havera and Nixon, 1978).

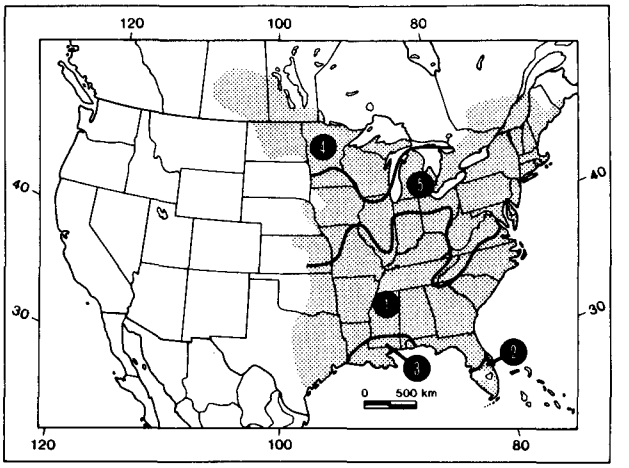

FIG. 3. Distribution of *Sciurus carolinensis* in North America; 1, *S. c. carolinensis*; 2, *S. c. extimus*; 3, *S. c. fuliginosus*; 4, *S. c. hypophaeus*; 5, *S. c. pennsylvanicus* (modified from Hall, 1981).

Mean heart rates of captive squirrels average 259 beats/min, but rates of free-ranging animals likely are lower; fear bradycardia of 25% occurs when cover is available (Smith and Johnson, 1984). The range of mean blood pressure parameters (Dunaway and Lewis, 1965; Guthrie et al., 1966, 1967; Hall, 1965; Hoff et al., 1976*a*) is: hematocrit, 32.7–44.2%; hemoglobin, 11.0–14.4 g/100 ml; red blood cell count, 6.6–7.3 × 10^6 cells/mm^3; red blood cell diameter, 6.67–6.85 μm; mean corpuscular volume (MCV), 58.0–66.7 μm^3; mean corpuscular hemoglobin (MCH), 19.6 pg; white blood cell count, 2,025–2,300 cells/mm^3. Males had higher hematocrit and hemoglobin levels than females (Guthrie et al., 1966, 1967). Platelet counts ranged from 7.1 × 10^5 cells/ml in autumn to 24.1 × 10^5 cells/ml in winter (Hoff et al., 1976*a*). Plasma glucose is 109–139 mg/100ml and plasma cholesterol is 143–248 mg/100ml (Guthrie et al., 1966, 1967; Hoff et al., 1976*b*). Serum pre-albumin levels are 4.3–9.5% (Wild, 1965).

Animals in traps may enter shock characterized by convulsions, variable respiratory and heart rates, low rectal temperature, and death. Hematological changes include severe hypoglycemia, leukopenia, lowered levels of adrenal glucocortocoids, elevated hematocrit and blood urine nitrogen levels (Guthrie et al., 1967; Hoff et al., 1976*b*).

Rectal temperatures are 36.4–38.7°C (Bolls and Perfect, 1972; Hoff et al., 1976*a*). Venous shunts at the base suggest the tail is used in thermoregulation (Thorington, 1966). Nonshivering thermogenesis accounts for 20–25% of cold-induced heat production with the remainder due to shivering (Ducharme et al., 1989). Cold-exposed eastern gray squirrels deprived of food and shelter lost 36% of body mass before death (Merson et al., 1978). Black animals at temperatures <−10°C have 18% lower heat loss, 20% lower basal metabolic rates, and a nonshivering thermogenesis capacity 11% higher than gray morphs (Ducharme et al., 1989; Innes and Lavigne, 1979). Metabolic rates range from 0.014–0.017 kJ/g/h during summer to 0.020–0.024 kJ/g/h during winter in Canada (Ducharme et al., 1989; Innes and Lavigne, 1979). Metabolic rates are 1.5–4 times higher than expected based on body size (Ducharme et al., 1989; Reynolds, 1985*a*). Juvenile metabolic rates are 1.8 times greater than adult rates (Knee, 1983). Lower critical temperature is 20–25°C. Nonshivering thermogenesis is twice as great in cold acclimated than warm acclimated eastern gray squirrels in Canada. Metabolic rates of cold-exposed *S. carolinensis* are 13.5 times the predicted standard metabolic rate, among the best performances of homeotherms (Ducharme et al., 1989). The respiratory quotient is 0.78 (Bolls and Perfect, 1972). Metabolizable energy requirements in autumn are 699 $kJkg^{-0.75}day^{-1}$ (Ludwick et al., 1969). Energy assimilation rates are 345–715 kJ/squirrel/day. Food consumption peaks in summer or autumn and decreases in winter (Knee, 1983). Eastern gray squirrels consumed twice as much food at <4°C as individuals at 24°C (Merson et al., 1978). Females tend to consume more food than males (Short and Duke, 1971). Autumn rates of food consumption exceeded energetic needs by 32% (Ludwick et

al.,1969) and daily assimilation rates generally exceed yearly averages (Knee, 1983). Assimilation efficiencies range from 72% for lab chow to 95% for shagbark hickory (*Carya ovata*; Ludwick et al., 1969; Knee, 1983; Montgomery et al., 1975). Body mass follows trends in food consumption with maxima in autumn or winter and minima in spring or summer (Knee, 1983).

The ocular lens is disc-shaped, averages 6 mm in diameter, is composed of about 32% protein, and possesses yellow, low molecular weight, and water-soluble pigments with peak absorption at 370 nm; pigments filter blue and near-ultraviolet light to protect the retina (Flyger and Gates, 1982; Zigman et al., 1985). The retina contains 40% rod-like receptors; the separate function of photoreceptors permit photopic and scotopic (Green and Dowling, 1975; West and Dowling, 1975) as well as red/green color vision (MacDonald, 1992).

Brain mass averages 7.76 g (Meier, 1983). The auditory region detects frequencies of 33–190 Hz and the primary auditory area has reversed orientation (Merzenich et al., 1976). The visual system has ≥5 cortical visual areas; the diurnal, arboreal environment possibly favored enlarged occipital and temporal areas (Gould, 1984).

The mass of adrenal glands averages 0.14 g; mean kidney fat indices average 2.1; three Pennsylvania individuals had a single kidney and adrenal gland (Allen, 1982). Urine pH of Florida individuals averaged 6.4 with protein content of 131 mg/100 ml; ketonuria, glucosuria, and bilirubinuria are known (Hoff et al., 1976*b*). Thyroid glands of Indiana juveniles (mean = 6.1 mg/100 g body mass) weigh relatively more than those of adults (mean = 5.5 mg/100 g body mass) probably due to the high metabolic rate necessary for somatic growth (Hoffman and Kirkpatrick, 1960).

Individuals are aged in the field (juvenile <6 months, subadult 6–12 months, adult >1.0 year) by coloration of genitals and mammae, tail molt pattern and pigmentation, and pattern of pigmentation on body pelage (Larson and Taber, 1980). These characters are most useful in autumn when age-class differences are greatest but may overestimate age in years of precocious reproduction (Hoffman and Kirkpatrick, 1959). In the laboratory, mass of eye lens, closure of epiphyses (Larson and Taber, 1980), cementum annuli (Fogl and Mosby, 1978), toothwear and replacement (Hench et al., 1984), and suspensory tuberosities (Colburn, 1986) are used to age individuals.

ONTOGENY AND REPRODUCTION. The duplex uterus of specimens from England and Ohio averages 81.0 mm long and the coiled oviducts 0.6 cm long (Deanesley and Parkes, 1933; Nixon and McClain, 1975). Mean os clitoridis length is 3.6 mm (Burt, 1960). Ovulation is induced by the presence of a fertile male (Webley and Johnson, 1983). Ova are 95 μm in diameter (Deanesley and Parkes, 1933); implantations are evenly distributed in uterine horns (Shorten, 1951). The paraplacental chorion allows albumin to diffuse but restricts large proteins (Wild, 1971). Placental scars remain for >7 week (Nixon and McClain, 1975).

Females may bear young at 5.5 months of age in North Carolina (Smith and Barkalow, 1967), but most do not reproduce until >1.25 year (Brauer and Dusing, 1961; Brown and Yeager, 1945); reproductive longevity is >8.0 year and possibly 12.5 year in North Carolina (Barkalow and Soots, 1975). The vagina is closed in anestrous and prepubescent females. An enlarged pink vulva indicates estrus; behavioral estrus lasts <8 h (Thompson, 1977*a*). Most breeding occurs in December–February and May–June in Illinois (Brown and Yeager, 1945) and is delayed slightly in northern latitudes (Shorten, 1951). In South Africa, similar seasonality begins with spring breeding in October (Millar, 1980). Gestation is 44 days (Webley and Johnson, 1983).

Males follow females 5 days before estrus (Thompson, 1977*a*). As many as 34 males are attracted to an estrous female (Goodrum, 1961) from distances ≤500 m (Thompson, 1977*a*). A dominance hierarchy forms among males; females mate with several males (Koprowski, 1993*a*). Copulation lasts <30 seconds and the male mounts dorsally (Koprowski, 1993*a*); a gelatinous white vaginal plug forms after ejaculation (Deanesley and Parkes, 1933; Koprowski, 1992).

Plasma progesterone rises from <3 nmol/l before gestation to 318 nmol/l in day 35 of gestation; levels drop after parturition (Tait et al., 1981). Ovaries of pregnant females weigh nearly twice those of non-pregnant females; ovarian follicles are numerous and largest in pregnancy (Cowles et al., 1977). Corpora lutea regress at day 30 of pregnancy. The corpora lutea and placenta are the sources of progesterone (Tait et al., 1981); however, pregnancy continues after ovariectomy >day 16 (Webley and Johnson, 1982). The highest levels of androstenedione are in estrous females (Webley et al., 1984).

The number of corpora lutea usually is equal to the number of embryos. Combined ovum and embryo mortality was about 9% in Ohio (Nixon and McClain, 1975). Average litter sizes range from 1.8 to 3.7 with a mode of 2–3 (Barkalow et al., 1970; Brown and Yeager, 1945; Deanesley and Parkes, 1933; Nixon et al., 1975) and a maximum of eight (Barkalow, 1967). In Ohio, the five-year average percentage of adults producing litters for spring was 61% (range, 0–95%) and for summer was 66% (range, 9–100%). About 90% of adults, 50–60% of yearlings, and <5% of subadults and juveniles (<1 year) reproduce each year in Ohio; two litters were produced in a year by 27% (range, 0–36%) of adult females (Nixon and McClain, 1975). Litter size dropped from 2.6 in a year with abundant food to 1.8 in year of food scarcity in North Carolina (Barkalow et al., 1970). Frequency of lactation in summer fell from 86% to 3% after a mast failure (Nixon and McClain, 1969). In a year with a good mast crop, 36% of females produced two litters while none did so in years of mast failure (Nixon and McClain, 1975). Precocious breeding by females is observed only after a good mast crop (Nixon and McClain, 1975; Smith and Barkalow, 1967).

The baculum is 9.2–12.3 mm long (Burt, 1960). Males are sexually mature at 10–11 months of age in Indiana (Kirkpatrick and Hoffman, 1960); however, maturation of young males housed with adult males is delayed until 2 years (Webley et al., 1985). Males undergo a semiannual cycle of testicular recrudescence and regression; functional testes are pendant in the scrotum. Spermatogenesis usually occurs December–February and May–July (Webley and Johnson, 1983). Regressed testes without spermatogenesis usually occur in August–October (Webley and Johnson, 1983) and last 2 months/individual (Kirkpatrick and Hoffman, 1960; Webley et al., 1985). Active testes weigh 6–7 g versus 1 g for inactive testes (Webley and Johnson, 1983). Entire breeding seasons occasionally may be skipped (Dubock, 1979*b*; Webley et al., 1985).

The interstitial cells of Leydig atrophy in regressed testes and result in lowered plasma androgen levels (Pudney and Lacy, 1977). Mean plasma testosterone levels in spermatogenically active males were 0.80–7.00 nmol/l but ≤0.05 nmol/l in regressed males (Webley et al., 1984). Testosterone levels vary from 0.4 to 20.0 nmol/l and peak late in the day. Testosterone declines to undetectable levels 3 weeks after castration with a concomitant fall in accessory gland weights (Webley et al., 1985). Progesterone is produced in the seminiferous tubules and accumulates in regressed testes (Pudney and Lacy, 1977). Regrowth of the prostate is preceded by mitotic activity (Siwela and Tam, 1984). The prostate has either two types of secretory cells or a single type that changes function seasonally (Siwela and Tam, 1984). Only 42% of germ cells become spermatozoa, resulting in relatively low numbers of spermatozoa for rodents (Tait and Johnson, 1982). Epididymal spermatozoa aggregate into unique cylindrical bodies and then separate, becoming single or rouleaux (Martan et al., 1970).

Neonates are naked except for vibrissae and weigh 13–18 g. The umbilicus is attached for ≤4 days. The dorsum darkens at 7–10 days preceding the emergence of hair. Hair occurs on the tail dorsum by 3 weeks and the ventral surface by 6 weeks. Eyes open at 24–42 days; ears open at 3–4 weeks. Lower incisors erupt at 19–21 days followed by upper incisors in week 4 and cheek teeth in week 6. Weaning beings at 7 weeks and is complete by 10 weeks. The juvenile pelage is lost after weaning. Adult body mass is reached after 8–9 months (Horwich, 1972; Shorten, 1951).

ECOLOGY. Eastern gray squirrels are most common in mature continuous woodlands >40 ha with a diverse woody understory. Densities are highest in habitats composed of tree species that produce winter-storable foods such as oak (*Quercus*), hickory (*Carya*), and walnut (*Juglans*; Brown and Batzli, 1984; Nixon and Hansen, 1987). Due to the variability in seed production, a diversity of nut trees is important to support high densities (Nixon and Hansen, 1987).

Formation of den cavities requires 8–30 years (Baumgartner, 1939). A minimum of 1 den/0.8 ha is required to maintain a density of 1 squirrel/1.6 ha (Sanderson, 1975). Addition of artificial nests increases densities (Nixon and Donohoe, 1979). Selective cutting ≤55% of the basal area of trees ≥30.5 cm diameter at breast height had little effect on densities, reproduction, or survival 1–2 year post-cut except for a temporary decrease in female survival

(Nixon et al., 1980*a*). Female recovery rates were half those of males in a large clear cut. Small (<8 ha), narrow (<160 m) clear cuts did not change any population parameters (Nixon et al., 1980*b*).

Densities of eastern gray squirrels are usually <3/ha in continuous woodlands in North Carolina (Barkalow et al., 1970), while densities in small (<10 ha) woodlots can be 16/ha (Doebel and McGinnes, 1974) and in urban parks can be >21/ha (Manski et al., 1981). Densities vary with fluctuations in the availability of tree seeds (Nixon and McClain, 1969), but long-term densities remain constant (Gurnell, 1987). Food may be limited in winter if autumn nut crops are exhausted and late spring–early summer if spring fruits are exhausted (Koprowski, 1991*a*). Winter feeding with corn does not increase survival (Havera and Nixon, 1980). After frost damage to tree tissues, eastern gray squirrel mass, survival, and reproduction decrease (Koprowski, 1991*a*; Nixon and McClain, 1969).

Home ranges vary from 0.5 to >20.2 ha, but are usually <5 ha (Don, 1983; Flyger and Gates, 1982). Home ranges of males are ≥1.2 times larger than those of females (Don, 1983; Heaney, 1984). Sexual activity best explains seasonal and annual differences in size of home range (Kenward, 1985). Home ranges are largest in spring and summer; female range sizes vary less than males by season (Kenward, 1985; Thompson, 1978*b*). Home range size is negatively correlated with density (Don, 1983). Space use by females may decrease nearly 50% during lactation (Kenward, 1985). Juvenile home ranges are smaller than adult males but may be equal to or larger than those of adult females (Don, 1983). A home range is used in the same sequence each day (Connolly, 1979). Eastern gray squirrels possess a strong homing tendency and may return from ≤4.5 km (Hungerford and Wilder, 1941).

Overlap of home ranges is extensive; territoriality is not evidenced (Don, 1983; Thompson, 1978*b*), although adults may defend core areas in autumn thereby limiting immigration (Kenward, 1985). Agonistic behavior peaks in spring and autumn, the periods of greatest dispersal (Thompson, 1978*b*). Natal dispersal may be male-biased (Cordes and Barkalow, 1972; Koprowski, 1991*b*; Taylor, 1969) or lack sex-bias (Thompson, 1978*b*). Males disperse long distances most frequently (Gurnell, 1987); the longest recorded movement is 100 km (Sharp, 1959). Aggressive juveniles and heterozygous color morphs were least likely to disperse (Pasitschniak-Arts and Bendell, 1990).

Sex ratios (male : female) vary from 0.93–1.07:1 in nestlings, 0.81–1.41:1 in juveniles, and 0.85–1.60:1 in adults (Flyger and Cooper, 1967; Gurnell, 1987; Mosby, 1969). Declining populations have fewer juveniles (44%) than stable or increasing populations (55–58%) (Barkalow et al., 1970; Mosby, 1969; Thompson, 1978*a*). Populations can sustain a hunting loss of ≤40%, but immigration sustained a population with an 80% loss (Mosby, 1969; Nixon et al., 1975).

Survivorship from <8 weeks to 1 year averages 25% (range, 2–68%) with no sex difference in North Carolina (Barkalow et al., 1970); survival of juveniles from weaning until 1 year was 34% for autumn-born and 37% for spring-born individuals in Canada (Thompson, 1978*a*). Mean annual mortality for adults ranges from 42–57% (Barkalow et al., 1970; Mosby, 1969; Thompson, 1978*a*). Annual mortality for each year of life beginning with the first is: 75%, 55%, 27%, 32%, 26%, 59%, 2%, 100% in North Carolina (Barkalow et al., 1970). Juvenile losses associated with dispersal contribute to high mortality during the first year of life (Barkalow et al., 1970; Cordes and Barkalow, 1972; Thompson, 1978*a*, 1978*b*). Dispersal peaks in April–May and July–October as subadults emigrate (Kenward, 1985; Thompson, 1978*a*). Turnover times (>99% of the population) were 6.2 and 6.3 year for unhunted populations (Barkalow et al., 1970; Mosby,1969). Maximum natural longevity is 12.5 years for females and 9.0 years for males in North Carolina (Barkalow and Soots, 1975); a captive female survived >20 years (Barkalow and Shorten, 1973). Seasonal survival varies markedly (20–100%/quarter); the cause of loss is rarely detected (Allen, 1982; Thompson, 1978*a*). Survival, particularly of juveniles, is related to the variation in tree seed availability with the extremes in crop size most influential (Koprowski, 1991*a*; Nixon and McClain, 1969; Nixon et al., 1975).

Predators include largemouth bass (*Micropterus salmoides*), timber (*Crotalus horridus*) and diamondback rattlesnakes (*C. adamanteus*), black rat snakes (*Elaphe obsoleta*; Moore, 1941), red-tailed hawk (*Buteo jamaicensis*), red-shouldered hawk (*B. lineatus*), goshawk (*Accipiter gentilis*), Cooper's hawk (*A. cooperii*), great horned owl (*Bubo virginianus*), barred owl (*Strix varia*), red squirrel (*Tamiasciurus hudsonicus*), weasel (*Mustela frenata*; Hamilton, 1934), mink (*M. vison*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), wolf (*Canis lupus*), coyote (*C. latrans*), dogs, and cats (Barkalow and Shorten, 1973; Gurnell, 1987; Packard, 1956). Fatal falls are rare (Thompson, 1976); however, Thorington (1972) reported 3 of 65 animals with mending long bones. Heavy-metals were high in kidneys from urban areas (McKinnon et al., 1976). A juvenile died from congenital aortic stenosis (Phillips and Dubielzig, 1980). Davidson (1976) and Flyger and Gates (1982) provide an extensive list of parasites including 6 protozoans, 2 trematodes, 10 cestodes, 1 acanthacephalan, 23 nematodes (Hugot, 1984; Parker et al., 1972), 37 mites and ticks (Britt and Molyneux, 1979; Whitaker et al., 1976), 7 lice, 17 fleas (Britt and Molyneux, 1979; Whitaker et al., 1976), and 1 dipteran. Bot flies (*Cuterebra emasculator*) parasitize eastern gray squirrels in autumn and larvae may infest 7 to >50% of individuals (Jacobson et al., 1979). Mange mite (*Notoedres, Sarcoptes,* and *Cnemidoptes*) infestations can cause death (Carlson et al., 1983; Flyger and Gates, 1982). Other reported diseases and causes of death include California encephalitis virus, pox-virus induced fibromas of the skin (Flyger and Gates, 1982), human echovirus 1/8 complex (Hoff et al., 1980), carciosarcoma mammary tumors (Shivaprasad et al., 1984), acute fatal toxoplasmosis (Roher et al., 1981), tularemia, tetanus, leptospirosis, and Q Fever (Flyger and Gates, 1982). Rabies is rare (Pritchett, 1938). Mouth and blood cultures revealed >8 bacteria genera (White et al., 1975). Ringworm (*Trichophyton mentagrophytes*) was among 19 genera of fungi isolated from epidermis (Flyger and Gates, 1982). Yersinosis (*Yersinia*) occurs (Keymer, 1983); systemic phycomycosis may cause death (Novilla et al.,1981).

Extensive migrations in which masses of moving eastern gray squirrels extended for >160 km and lasted for 3 weeks were reported in 1700s and 1800s. These migrations usually occurred in autumn, with *S. carolinensis* swimming large lakes and rivers possibly in response to food shortage (Schorger, 1949). Such movements also were reported in the 1900s (Schorger, 1949), most recently in 1968 in the eastern United States (Flyger, 1969). Emigration from a Lake Michigan island population in 1985 lasted 1 month with >90 drowned carcasses recovered (Long and Long, 1986).

Leaf nests average 47 l and consist of a platform of twigs on a tree limb, a compacted base of decaying matter, an outer shell of twigs and leaves, and usually a lining of shredded material. Summer leaf nests are not as robust as winter nests (Fitzwater and Frank, 1944). Cavities within trees are also used heavily; den cavities are used often in winter and leaf nests are used in warmer months (Nixon and Hansen, 1987).

Geographic ranges of *S. carolinensis* and the fox squirrel, *S. niger*, overlap extensively and syntopy is common (Armitage and Harris, 1982). Food preferences are similar (Smith and Follmer, 1972). *S. carolinensis* females are displaced from concentrated food sources by *S. niger* females in the breeding season but eastern gray squirrels are more efficient at finding food (Brown and Batzli, 1985*a*). Removal of adult female *S. niger* resulted in slight shifts in space use of female eastern gray squirrels (Brown and Batzli, 1985*b*). Eastern gray squirrels inhabit areas with thick understory and ground cover; large woodlots also tend to have high densities of understory vegetation and high eastern gray squirrel densities (Brown and Batzli, 1984; Nixon et al., 1978). *Tamiasciurus hudsonicus* are aggressors in encounters with *S. carolinensis*; however, the species will share a nest box when housed together (Ackerman and Weigl, 1970) and tolerance appears to be common in the field (Riege, 1991). In England, the range of *S. carolinensis* rapidly expanded while native *S. vulgaris* disappeared from colonized areas. The mechanism of the displacement is unclear. Competition is at best only a partial explanation because local extinctions often occur when only one species is present. Hypotheses that invoke habitat change and *S. carolinensis* as a disease vector also have little support (Reynolds, 1985*b*).

Although *S. carolinensis* feed on as many as 97 plant and 14 animal items, 18 plant species account for 87% of the volume while 62% of stomachs contain only one food in Missouri (Korschgen, 1981). Squirrels feed heavily on nuts, flowers, and buds of ≥24 oak species, 10 species of hickory and pecan, walnuts, and beech (*Fagus grandifolia*) when available (Korschgen, 1981; Nixon et al., 1968). Other important foods (Flyger and Gates, 1982; Goodrum, 1961; Korschgen, 1981; Nixon et al., 1968; Thompson and Thompson, 1980) include the fruits, seeds, buds, or flowers of maples (*Acer*), mulberry (*Morus*), hackberry (*Celtis*), elms (*Ulmus*), buckeye and horse chestnuts (*Aesculus*), wild cherries, (*Prunus*), dogwoods (*Cor-*

nus), hawthorn (*Crataegus*), black gum (*Nyssa sylvatica*), hazelnut (*Corylus americana*), hop hornbeam (*Ostrya virginiana*), and ginkgo (*Ginkgo biloba*). Seeds and catkins of gymnosperms are eaten, including cedar (*Juniperus*), hemlock (*Tsuga*), pines (*Pinus*), and spruce (*Picea*; Barkalow and Shorten, 1973; Thompson and Thompson, 1980). A variety of herbaceous species are eaten; fungi are readily eaten in summer. Cultivated crops such as corn and wheat are eaten especially in winter. Females ingest gravel and soil in winter and early spring (Korschgen, 1981; Nixon et al., 1968; Thompson and Thompson, 1980). Insects are eaten in summer and may be an important food for juveniles (Korschgen, 1981; Nixon, 1970). Other food items include bones (Flyger and Gates, 1982), bird eggs and nestlings (Bailey, 1923), and frogs (Goodrum, 1961). Cannibalism is reported (Holm, 1976; Thompson, 1976).

Historically, corn of Native Americans and early colonists suffered high losses to eastern gray squirrels (Schorger, 1949). *S. carolinensis* damage to trees by debarking is a serious problem in England but not in the United States (Gurnell, 1987). Squirrels ingest some bark and cambium (Packard, 1956) and phloem width is an important predictor of damage; juvenile density is positively correlated with damage (Kenward and Parish, 1986). Squirrels may gnaw through wooden walls and roof shingles; large quantities of napthalene or paradichlorobenzene (moth balls or crystals) may discourage use. Gnawing on trees may be reduced with tetramethylthiuram disulfide. Methyl nonyl ketone crystals and paradichlorobenzene may repel animals from garden and property borders; however, the effectiveness of these treatments is questionable (Jackson, 1983).

Squirrels can be live-trapped with box traps baited with peanuts, peanut butter, corn, sunflower seeds, or nuts (Baumgartner, 1940). Traps should be checked at least twice daily to prevent mortalities. Success is greatest in winter and spring (Dubock, 1979*a*; Perry et al., 1977) and at the base of large nut producing trees (Perry et al., 1977). Eastern gray squirrels can be flushed from traps into a wire mesh or cloth handling cone to restrict movements (Baumgartner, 1940). Methoxyflurane, an inhalant, provides a short-term anesthesia (Barry, 1972). *S. carolinensis* are temporarily marked with fur dyes (Fitzwater, 1943) or selective clipping of fur (Flyger, 1955). Semi-permanent identification is accomplished with ear tags (Baumgartner, 1940), ear tags with streamers (Koprowski et al., 1988), or color-coded collars (Wood, 1976). Permanent identification is possible using toe-clipping (Baumgartner, 1940), ear tattooing (Perry et al., 1977), freeze branding (Brown and Batzli, 1985*b*), or freeze marking (Koprowski, 1991*a*). There is no widely applicable method for estimating the abundance of eastern gray squirrels although mark-recapture methodologies are promising when used with sufficient trapping effort or in combination with standardized observations or hunter returns (Allen, 1982; Nixon et al., 1967).

As many as 2.5 million *S. carolinensis* are harvested annually in Mississippi with an economic impact of $12.5 million in this state alone (Flyger and Gates, 1982). *S. carolinensis* provided food for Native Americans and European colonists (Barkalow and Shorten, 1973; Schorger, 1949) and continue to be eaten by humans today. Squirrels rank second to songbirds in value to nature watchers (Shaw and Mangun, 1984).

Nestlings can be raised on milk followed by bread and milk, and finally soft fruits and vegetables as young are weaned (Crandall, 1964). Ducharme et al. (1989) maintained captives in cages >0.7 by 0.7 by 1.8 m high that were provisioned with a nest box, branches to gnaw, and a 10-cm layer of wood shavings. The weekly diet consisted of 300 to 400 g of shelled nuts (walnuts, filberts, almonds, and peanuts in a 2:2:2:1 mix) supplemented with apple, carrot, corncob, or mushrooms. Water with a vitamin supplement was available ad lib. Diets rich in sunflower seeds can cause osteodystrophy (Wallach and Hoff, 1982). Breeding in captivity is difficult because large (>0.25 ha) enclosures or long acclimation periods are necessary (Webley and Johnson, 1983).

BEHAVIOR. The diel activity pattern is bimodal in spring to autumn, peaking about 2 h after sunrise and 2–5 h before sunset; a unimodal pattern occurs in winter with a peak 2–4 h before sunset. Lowest activity is in winter, peak activity is in summer (Thompson, 1977*b*) or autumn (Bakken, 1959). *S. carolinensis* are active >70% of the daylight hours in summer compared to <35% in winter (Gurnell, 1987). Females may be more active than males in spring and summer; males are more active than females in autumn and winter (Bakken, 1959; Thompson, 1977*b*). Foraging peaks in autumn to spring at >75% while grooming and resting peak in summer at 10–30% of the active period (Erossy, 1973; Gurnell, 1987; Hampshire, 1985). Arboreal foraging peaks in summer when seeds and fruits ripen and declines in winter (Gurnell, 1987); arboreal activity in winter is energetically costly and likely to be avoided (Byman et al., 1988). High winds, heavy rain, snow cover, and extreme temperature decrease activity (Gurnell, 1987).

The ontogeny of behavior occurs in eight stages (Horwich, 1972). In the Postembryonic Period (<16 days), young nurse, eliminate wastes, and maintain a steady state using postural reflexes and orientation movements. The Preliminary Period (17–30 days) consists of uncoordinated movements and twitching; the Transition Period (30–40 days) is dominated by maintenance activities and early social behaviors. Locomotory and Socialization Periods (41–70 days) are characterized by a full behavior repertoire; weaning is completed. Juvenile and Subadult Periods (70 days–11 months) are dominated by home range expansion, increased aggression, and sexual play; the Adult Period begins at reproductive maturity.

Male eastern gray squirrels dominate females and adults dominate juveniles (Allen and Aspey, 1986). Residents are particularly aggressive toward immigrants; combat is rare but results in torn ears, broken tails, or body wounds (Bakken, 1959; Koprowski, 1991*b*, 1993*b*; Taylor, 1969; Thompson, 1978*a*, 1978*b*). The most common social behavior is group nesting in single and mixed-sex groups (Koprowski, 1991*b*; Taylor, 1969). Taylor (1969) suggests a complex social system of stable groups of potentially related animals that defend a discrete area. Amicable behaviors are directed towards close relatives (Koprowski, 1991*b*; Koprowski, 1993*b*). Pregnant females nest alone; lactating females are aggressive and avoided by others (Cordes and Barkalow, 1972; Hampshire, 1985; Nixon and McClain, 1975).

Males regularly visit traditional marking points on trees and deposit scent in urine and from glands in the oral-labial region after gnawing the area (Taylor, 1977). Both sexes mark substrate with oral gland secretions at non-traditional, dispersed sites while traversing their home ranges (Koprowski, 1993*c*). Neonates make lip-smacking noises and squeak calls. At 4 weeks, growls, muk-muks, and screams or combinations are used. Tooth chattering occurs in agonistic interactions. Four notes are used in alarm vocalizations: buzz, kuk, moan, and quaa (Gurnell, 1987).

S. carolinensis swim by a dog-paddle with head out of water (Barkalow and Shorten, 1973). Speeds of 27 km/h are attained while galloping (Layne and Benton, 1954). Most feeding is in a bipedal stance while manipulating items in the forepaws. Vigilance is usually by a bipedal stance with varying erectness (Fig. 1). Squirrels are adept climbers; climbing is accomplished with a trot or gallop.

Eastern gray squirrels are classic scatterhoarders. Nuts are carried in the jaws and buried <2 cm below the soil surface (Vander Wall, 1990). The taproot of white oak acorns is excised to prevent overwinter germination; this behavior is learned (Fox, 1982). Olfaction and memory are important in locating buried nuts (Jacobs and Liman, 1991). Olfactory cues are important in selection of food items (Vander Wall, 1990). Acorns with high lipid content are preferred (Smith and Follmer, 1972); however, large amounts of tannins can cause refusal of nuts with high lipid content (Smallwood and Peters, 1986). Food preferences suggest squirrels forage to maximize energy gain (Smith and Follmer, 1972) and forage in patches with high rates of energy intake (Lewis, 1980); however, high tannin content or predation risk are known constraints (Lima and Valone, 1986; Smallwood and Peters, 1986). As distance from cover increases, flight distance increases (Dill and Houtman, 1989) and time spent moving between patches and feeding decreases (Newman et al., 1988).

GENETICS. The diploid number is 40; the fundamental number is 76 (Nadler and Sutton, 1967). 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 in 23 of 35 enzyme systems (Moncrief, 1993), although Havera and Nixon (1978) reported lower levels of variation. The few observations on the offspring of crosses between color morphs suggest that alleles for albinism segregate in simple Mendelian fashion with normal coloration completely dominant; alleles for melanism suggest a more complicated mode of inheritance (Shorten, 1951). Male *S. niger* follow female *S. carolinensis* in estrus but do not attempt to copulate (Koprowski, 1991*c*); hybridization is unknown (Gurnell, 1987).

REMARKS. *Sciurus* is from the ancient Greek, *skia* meaning shadow or shade, and *oura* for tail; *carolinensis* refers to the type locality of the colony of Carolina. Additional common names are cat squirrel and migratory squirrel (Flyger and Gates, 1982). I thank C. M. Nixon, R. M. Timm, and an anonymous reviewer for improving the manuscript. S. Hagen completed the figures.

LITERATURE CITED

ACKERMAN, R., AND P. D. WEIGL. 1970. Dominance relations of red and grey squirrels. Ecology, 51:332–334.

AHL, A. S. 1987. Relationship of vibrissal length and habits in the Sciuridae. Journal of Mammalogy, 68:848–853.

ALLEN, D. S. 1982. Social status and survivorship in a population of eastern gray squirrels (*Sciurus carolinensis*). Ph.D. dissert., Ohio State University, Columbus, 132 pp.

ALLEN, D. S., AND W. P. ASPEY. 1986. Determinants of social dominance in eastern gray squirrels (*Sciurus carolinensis*): a quantitative assessment. Animal Behaviour, 34:81–89.

ARMITAGE, K. B., AND K. S. HARRIS. 1982. Spatial patterning in sympatric populations of fox and gray squirrels. The American Midland Naturalist, 108:389–397.

AUDUBON, J. J., AND J. BACHMAN. 1849. The viviparous quadrupeds of North America. V. G. Audubon, New York, 383 pp.

BACHMAN, J. 1839. Monograph of the species of squirrel inhabiting North America. Proceedings of the Zoological Society of London, 1838:85–103.

BAILEY, B. 1923. Meat-eating propensities of some rodents of Minnesota. Journal of Mammalogy, 4:129.

BAKKEN, A. 1959. Behavior of gray squirrels. Proceedings of the Southeastern Association of Game and Fish Commissioners, 13:393–406.

BANGS, O. 1896. A review of the squirrels of eastern North America. Proceedings of the Biological Society of Washington, 10:145–167.

BARKALOW, F. S., JR. 1967. A record gray squirrel litter. Journal of Mammalogy, 48:141.

BARKALOW, F. S., JR., R. B. HAMILTON, AND R. F. SOOTS, JR. 1970. The vital statistics of an unexploited gray squirrel population. The Journal of Wildlife Management, 34:489–500.

BARKALOW, F. S., JR., AND M. SHORTEN. 1973. The world of the gray squirrel. J. B. Lippincott Company, Philadelphia, 160 pp.

BARKALOW, F. S., JR., AND R. F. SOOTS, JR. 1975. Life span and reproductive longevity of the gray squirrel, *Sciurus c. carolinensis* Gmelin. Journal of Mammalogy, 56:522–524.

BARNETT, R. J. 1977. Bergmann's rule and variation in structures related to feeding in the gray squirrel. Evolution, 31:538–545.

BARRY, W. J. 1972. Methoxyflurane: an anesthetic for field and laboratory use on squirrels. The Journal of Wildlife Management, 36:992–993.

BAUMGARTNER, L. L. 1939. Fox squirrel dens. Journal of Mammalogy, 20:456–465.

———. 1940. Trapping, handling, and marking fox squirrels. The Journal of Wildlife Management, 4:444–450.

BOLLS, N. J., AND J. R. PERFECT. 1972. Summer resting metabolic rate of the gray squirrel. Physiological Zoology, 45:54–59.

BRAUER, A., AND A. DUSING. 1961. Seasonal cycles and breeding seasons of the gray squirrel, *Sciurus carolinensis* Gmelin. Transactions of the Kentucky Academy of Science, 22:16–27.

BRITT, D., AND D. H. MOLYNEUX. 1979. Parasites of grey squirrels in Cheshire, England. Journal of Parasitology, 65:408.

BROWN, B. W., AND G. O. BATZLI. 1984. Habitat selection by fox and gray squirrels: a multivariate analysis. The Journal of Wildlife Management, 48:616–621.

———. 1985*a*. Foraging ability, dominance relations and competition for food by fox and gray squirrels. Transactions of the Illinois State Academy of Science, 78:61–66.

———. 1985*b*. Field manipulations of fox and gray squirrel populations: how important is interspecific competition? Canadian Journal of Zoology, 63:2134–2140.

BROWN, L. G., AND L. E. YEAGER. 1945. Fox squirrels and gray squirrels in Illinois. Illinois Natural History Survey Bulletin, 23:449–536.

BURT, W. H. 1960. Bacula of North American mammals. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 113:1–75.

BYMAN, D., D. B. HAY, AND G. S. BAKKEN. 1988. Energetic costs of the winter arboreal microclimate: the gray squirrel in a tree. International Journal of Biometeorology, 32:112–122.

CARLSON, B. L., D. P. ROHER, AND S. W. NIELSEN. 1982. Notoedric mange in gray squirrels (*Sciurus carolinensis*). Journal of Wildlife Diseases, 18:347–348.

COLBURN, M. L. 1986. Suspensory tuberosities for aging and sexing squirrels. The Journal of Wildlife Management, 50: 456–459.

CONNOLLY, M. S. 1979. Time-tables in home range usage by gray squirrels (*Sciurus carolinensis*). Journal of Mammalogy, 60: 814–817.

CORDES, C. L., AND F. S. BARKALOW, JR. 1972. Home range and dispersal in a North Carolina gray squirrel population. Proceedings of the Southeastern Association of Game and Fish Commissioners, 26:124–135.

COWLES, C. J., R. L. KIRKPATRICK, AND J. O. NEWELL. 1977. Ovarian follicular changes in gray squirrels as affected by season, age, and reproductive state. Journal of Mammalogy, 58:67–73.

CRANDALL, L. S. 1964. The management of wild mammals in captivity. University of Chicago, Chicago, 769 pp.

CURRADO, I., P. L. SCARAMOZZINO, AND G. BRUSSINO. 1987. Note sulla presenza dello scoiattolo grigio (*Sciurus carolinensis* Gmelin, 1788) in Piemonte. Annali della Facoltā di Scienze Agrariédella Universitā di Torino, 14:307–331.

DAVIDSON, W. R. 1976. Endoparasites of selected populations of gray squirrels (*Sciurus carolinensis*) in the southeastern United States. Proceedings of the Helminthological Society of Washington, 43:211–217.

DANIEL, H. J., III, AND L. K. ROBERSON. 1987. The ossicles of the eastern gray squirrel, *Sciurus carolinensis*. Journal of the Elisha Mitchell Scientific Society, 103:21–27.

DEANESLEY, R., AND A. S. PARKES. 1933. The reproductive processes of certain mammals. Part IV. The oestrus cycle of the gray squirrel (*Sciurus carolinensis*). Philosophical Transactions of the Royal Society of London B, 22:47–96.

DILL, L. M., AND R. HOUTMAN. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). Canadian Journal of Zoology, 67:233–235.

DOEBEL, J. H., AND B. S. MCGINNES. 1974. Home range and activity of a gray squirrel population. The Journal of Wildlife Management, 38:860–867.

DON, B. A. C. 1983. Home range characteristics and correlates in tree squirrels. Mammal Review, 13:123–132.

DUBOCK, A. C. 1979*a*. Male grey squirrel (*Sciurus carolinensis*) reproductive cycles in Britain. Journal of Zoology (London), 188:41–51.

———. 1979*b*. Methods of age determination in grey squirrels, *Sciurus carolinensis*, in Britain. Journal of Zoology (London), 188:27–40.

DUCHARME, M. B., J. LAROCHELLE, AND D. RICHARD. 1989. Thermogenic capacity in gray and black morphs of the gray squirrel, *Sciurus carolinensis*. Physiological Zoology, 62:1273–1292.

DUNAWAY, P. B. 1969. "Perfect" polydactylism in hind feet of a gray squirrel. The American Midland Naturalist, 81:244–247.

DUNAWAY, P. B., AND L. L. LEWIS. 1965. Taxonomic relation of erythrocyte count, mean corpuscular volume, and body-weight in mammals. Nature, 205:481–484.

EROSSY, P. J. 1973. Home range and social organization of a free-ranging population of gray squirrels (*Sciurus carolinensis*). M.S. thesis, Bowling Green State University, Bowling Green, Ohio, 68 pp.

FITZWATER, W. D., JR. 1943. Color marking of mammals with special reference to squirrels. The Journal of Wildlife Management, 7:190–192.

FITZWATER, W. D., JR., AND W. J. FRANK. 1944. Leaf nests of gray squirrels in Connecticut. Journal of Mammalogy, 25:160–170.

FLYGER, V. 1955. Implications of social behavior in gray squirrel management. Transactions of the North American Wildlife and Natural Resources Conference, 20:381–389.

———. 1969. The 1968 squirrel 'migration' in the eastern United States. Transactions of the Northeast Section of the Wildlife Society, 26:69–79.

FLYGER, V., AND H. R. COOPER. 1967. The utilization of nesting

boxes by gray squirrels. Proceedings of the Southeastern Association of Game and Fish Commissioners, 21:113–117.

FLYGER, V., AND J. E. GATES. 1982. Fox and gray squirrels. Pp. 209–229 *in* Wild mammals of North America (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins University Press, Baltimore, 1147 pp.

FOGL, J. G., AND H. S. MOSBY. 1978. Aging gray squirrels by cementum annuli in razor-sectioned teeth. The Journal of Wildlife Management, 42:444–448.

FOX, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. Evolution, 36:800–809.

GAPPER,–. 1830. Observations on the quadrupeds found in the district of upper Canada extending between York and Lake Simcoe, with the view of illustrating their geographical distribution as well as of describing some species hitherto unnoticed. Zoological Journal, 5:201–207. (Not seen, cited in Hall, 1981.)

GMELIN, J. F. 1788. Caroli a Linne Systema naturae. 13th edition. George Emanuel Beer, Leipzig, 4120 pp. (not seen, cited in Hall, 1981.)

GOODRUM, P. D. 1961. The gray squirrel in Texas. Texas Parks and Wildlife Department Bulletin, 42:1–43.

GOULD, H. J., III. 1984. Interhemispheric connections of the visual cortex in the grey squirrel (*Sciurus carolinensis*). Journal of Comparative Neurology, 223:259–301.

GREEN, D. G., AND J. E. DOWLING. 1975. Electrophysiological evidence for rod-like receptors in the grey squirrel, ground squirrel and prairie dog retinas. Journal of Comparative Neurology, 159:461–472.

GURNELL, J. C. 1987. The natural history of squirrels. Facts on File, New York, 201 pp.

GUTHRIE, D. R., H. S. MOSBY, AND J. C. OSBORNE. 1966. Hematological values for the eastern gray squirrel (*Sciurus carolinensis*). Canadian Journal of Zoology, 44:323–327.

GUTHRIE, D. R., J. C. OSBORNE, AND H. S. MOSBY. 1967. Physiological changes associated with shock in confined gray squirrels. Journal of Wildlife Management, 31:102–108.

GUTHRIE, W. 1815. A new universal geographical, historical, and commercial grammar. Philadelphia, 603 pp. (Not seen, cited in Hall, 1981.)

HALL, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, 1:1–600 + *90*.

HALL, F. G. 1965. Hemoglobin and oxygen: affinities in seven species of Sciuridae. Science, 148:1350–1351.

HAMILTON, W. J., JR. 1934. Red squirrel killing young cottontail and young gray squirrel. Journal of Mammalogy, 15:322.

HAMPSHIRE, R. J. 1985. A study on the social and reproductive behaviour of captive grey squirrels (*Sciurus carolinensis*). Ph.D. dissert., University of Reading, Reading, England, 246 pp.

HAVERA, S. P., AND C. M. NIXON. 1978. Geographic variation of Illinois gray squirrels. The American Midland Naturalist, 100: 396–407.

———. 1980. Winter feeding of fox and gray squirrel populations. The Journal of Wildlife Management, 44:41–55.

HEANEY, L. R. 1984. Climatic influences on the life-history tactics and behavior of the North American tree squirrels. Pp. 43–78 *in* The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

HEFNER, J. M. 1971. Age determination of the gray squirrel. M.S. thesis, Ohio State University, Columbus, 51 pp.

HENCH, J. E., G. L. KIRKLAND, JR., H. W. SETZER, AND L. W. DOUGLASS. 1984. Age classification for the gray squirrel based on eruption, replacement, and wear of molariform teeth. The Journal of Wildlife Management, 48:1409–1414.

HOFF, G. L., W. J. BIGLER, F. M. WELLINGS, AND A. L. LEWIS. 1980. Human enteroviruses and wildlife: isolation from gray squirrels. Journal of Wildlife Diseases, 16:131–133.

HOFF, G. L., E. B. LASSING, M. S. CHAN, W. J. BIGLER, AND T. J. DOYLE. 1976*a*. Hematologic values for free-ranging urban gray squirrels (*Sciurus c. carolinensis*). American Journal of Veterinary Research, 37:99–101.

HOFF, G. L., L. E. MCELDOWNING, W. J. BIGLER, L. J. KUHNS, AND J. A. TOMAS. 1976*b*. Blood and urinary values in the gray squirrel. Journal of Wildlife Diseases, 12:349–352.

HOFFMAN, R. A., AND C. M. KIRKPATRICK. 1959. Current knowledge of tree squirrel reproductive cycles and development. Proceedings of the Southeastern Association of Game and Fish Commissioners, 13:363–367.

———. 1960. Seasonal changes in thyroid gland morphology of male gray squirrels. The Journal of Wildlife Management, 24:421–425.

HOLM, R. F. 1976. Observations on a cannibalistic gray squirrel. Natural History Miscellanea, 197:1–2.

HORWICH R. H. 1972. The ontogeny of social behavior in the gray squirrel (*Sciurus carolinensis*). Advances in Ethology, 8:1–103.

HUGOT, J. P. 1984. Sur le genre *Trypanoxyuris* (Oxyuridae, Nematoda) I. Parasites de Sciurides: sous-genre *Rodentoxyuris*. Bulletin du Museum National d'histoire Naturelle (Paris), 6:711–720.

HUNGERFORD, K. E., AND N. G. WILDER. 1941. Observations on the homing behavior of the gray squirrel (*Sciurus carolinensis*). The Journal of Wildlife Management, 5:458–460.

INNES, S., AND D. M. LAVIGNE. 1979. Comparative energetics of coat colour polymorphs in the eastern gray squirrel, *Sciurus carolinensis*. Canadian Journal of Zoology, 57:585–592.

JACKSON, J. J. 1983. Tree squirrels. Pp. B141–B146, *in* Prevention and control of wildlife damage (R. M. Timm, ed.). Great Plains Agricultural Council, Lincoln, unpaged.

JACOBS, L. F., AND E. R. LIMAN. 1991. Grey squirrels remember the locations of buried nuts. Animal Behaviour, 41:103–110.

JACOBSON, H. A., D. C. GUYNN, AND E. J. HACKETT. 1979. Impact of the botfly on squirrel hunting in Mississippi. Wildlife Society Bulletin, 7:46–48.

JENKINS, F. A., JR., AND D. MCCLEARN. 1984. Mechanisms of hind foot reversal in climbing mammals. Journal of Morphology, 182:197–219.

KENWARD, R. E. 1985. Ranging behavior and population dynamics in grey squirrels. Symposia of the British Ecological Society, 25:319–330.

KENWARD, R. E., AND T. PARISH. 1986. Bark-stripping by grey squirrels (*Sciurus carolinensis*). Journal of Zoology (London), 210:473–481.

KEYMER, I. F. 1983. Diseases of squirrels in Britain. Mammal Review, 13:155–158.

KIRKPATRICK, C. M., AND R. A. HOFFMAN. 1960. Ages and reproductive cycles in a male gray squirrel population. The Journal of Wildlife Management, 24:218–221.

KNEE, C. 1983. Squirrel energetics. Mammal Review, 13:113–122.

KOPROWSKI, J. L. 1991*a*. Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. Journal of Mammalogy, 72:367–372.

———. 1991*b*. The evolution of sociality in tree squirrels: the comparative behavioral ecology of fox squirrels and eastern gray squirrels. Ph.D. dissert., University of Kansas, Lawrence, 117 pp.

———. 1991*c*. Mixed-species mating chases of fox squirrels and gray squirrels. Canadian Field-Naturalist, 105:117–118.

———. 1992. Removal of copulatory plugs by female tree squirrels. Journal of Mammalogy, 73:572–576.

———. 1993*a*. Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job." Behavioral Ecology, 4:165–171.

———. 1993*b*. The role of kinship in field interactions among juvenile gray squirrels (*Sciurus carolinensis*). Canadian Journal of Zoology, 71:224–226.

———. 1993*c*. Sex and species biases in scent marking by fox squirrels and eastern gray squirrels. Journal of Zoology (London), 230:319–323.

KOPROWSKI, J. L., J. L. ROSEBERRY, AND W. D. KLIMSTRA. 1988. Longevity records for the fox squirrel. Journal of Mammalogy, 69:383–384.

KORSCHGEN, L. J. 1981. Foods of fox and gray squirrels in Missouri. The Journal of Wildlife Management, 45:260–266.

KURTEN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 pp.

LARSON, J. S., AND R. D. TABER. 1980. Criteria of sex and age. Pp. 143–202, *in* Wildlife management techniques manual (S. D. Schemnitz, ed.). Fourth ed. The Wildlife Society, Washington, D.C., 686 pp.

LAYNE, J. N., AND A. H. BENTON. 1954. Some speeds of small mammals. Journal of Mammalogy, 35:103–104.

LEWIS, A. R. 1980. Patch use by gray squirrels and optimal foraging. Ecology, 61:1371–1379.

LIMA, S. L., AND T. J. VALONE. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. Animal Behaviour, 34:536–544.

LLOYD, H. G. 1983. Past and present distribution of red and grey squirrels. Mammal Review, 13:69–80.

LONG, C. A., AND J. E. LONG. 1986. Mass drowning of gray squirrels off Washington Island, Lake Michigan. The Jack-Pine Warbler, 64:21–22.

LUDWICK, R. L., J. P. FONTENOT, AND H. S. MOSBY. 1969. Energy metabolism of the eastern gray squirrel. The Journal of Wildlife Management, 33:569–575.

MACDONALD, I. M. V. 1992. Grey squirrels discriminate red from green in a foraging situation. Animal Behaviour, 43:694–695.

MANSKI, D. A., L. W. VANDRUFF, AND V. FLYGER. 1981. Activities of gray squirrels and people in a downtown Washington, D.C. park: management implications. Transactions of the North American Wildlife and Natural Resources Conference, 46: 439–454.

MARTAN, J., C. S. ADAMS, AND B. L. PERKINS. 1970. Epididymal spermatozoa of two species of squirrel. Journal of Mammalogy, 51:376–378.

MCGRATH, G. 1987. Relationships of nearctic tree squirrels of the genus *Sciurus*. Ph.D. dissert., University of Kansas, Lawrence, 101 pp.

MCKINNON, J. L., G. L. HOFF, W. J. BIGLER, AND E. C. PRATHER. 1976. Heavy metal concentrations in kidneys of urban gray squirrels. Journal of Wildlife Diseases, 12:367–371.

MEIER, P. T. 1983. Relative brain size within the North American Sciuridae. Journal of Mammalogy, 64:642–647.

MERRIAM, C. H. 1886. Preliminary description of a new squirrel from Minnesota (*Sciurus carolinensis hypophaeus*, sp. nov.). Science, 7:351.

MERSON, M. H., C. J. COWLES, AND R. L. KIRKPATRICK. 1978. Characteristics of captive gray squirrels exposed to cold and food deprivation. The Journal of Wildlife Management, 42: 202–205.

MERZENICH, M. M., J. H. KAAS, AND G. LINN ROTH. 1976. Auditory cortex in the grey squirrel: tonotopic organization and architectonic fields. Journal of Comparative Neurology, 166: 387–401.

MILLAR, J. C. G. 1980. Aspects of the ecology of the American grey squirrel *Sciurus carolinensis* Gmelin in South Africa. M.S. thesis, University of Stellenbosch, South Africa, 313 pp.

MONCRIEF, N. D. 1993. Geographic variation in fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) of the lower Mississippi river valley. Journal of Mammalogy, 74:547–576.

MONTGOMERY, S. D., J. B. WHELAN, AND H. S. MOSBY. 1975. Bioenergetics of a woodlot gray squirrel population. The Journal of Wildlife Management, 39:709–717.

MOORE, G. C. 1941. Prey chases predator. Journal of Mammalogy, 22:198.

MOSBY, H. S. 1969. The influence of hunting on the population dynamics of a woodlot gray squirrel population. The Journal of Wildlife Management, 33:59–73.

NADLER, C. F., AND D. A. SUTTON. 1967. Chromosomes of some squirrels (Mammalia-Sciuridae) from the genera *Sciurus* and *Glaucomys*. Experientia, 24:249–251.

NERO, R. W. 1958. Additional gray squirrel information. The Blue Jay, 16:80.

NEWMAN, J. A., G. M. RECER, S. M. ZWICKER, AND T. CARACO. 1988. Effects of predation hazard on foraging "constraints": patch-use strategies in grey squirrels. Oikos, 53:93–97.

NIXON, C. M. 1970. Insects as food for juvenile gray squirrels. The American Midland Naturalist, 84:283.

NIXON, C. M., AND R. W. DONOHOE. 1979. Squirrel nest boxes—are they effective in young hardwood stands? Wildlife Society Bulletin, 7:283–284.

NIXON, C. M., AND L. P. HANSEN. 1987. Managing forests to maintain populations of gray and fox squirrels. Illinois Department of Conservation Technical Bulletin, 5:1–35.

NIXON, C. M., AND W. J. HARPER. 1972. Composition of gray squirrel milk. Ohio Journal of Science, 72:3–6.

NIXON, C. M., AND M. W. MCCLAIN. 1969. Squirrel population decline following a late spring frost. The Journal of Wildlife Management, 33:353–357.

———. 1975. Breeding seasons and fecundity of female gray squirrels in Ohio. The Journal of Wildlife Management, 39: 426–438.

NIXON, C. M., W. R. EDWARDS, AND L. EBERHARDT. 1967. Estimating squirrel abundance from live-trapping data. The Journal of Wildlife Management, 31:96–101.

NIXON, C. M., S. P. HAVERA, AND R. E. GREENBERG. 1978. Distribution and abundance of the gray squirrel in Illinois. Biological Notes, Illinois Natural History Survey, 105:1–55.

NIXON, C. M., S. P. HAVERA, AND L. P. HANSEN. 1980*a*. Initial response of squirrels to forest changes associated with selection cutting. Wildlife Society Bulletin, 8:298–306.

NIXON, C. M., M. W. MCCLAIN, AND R. W. DONOHOE. 1975. Effects of hunting and mast crops on a squirrel population. The Journal of Wildlife Management, 39:1–25.

———. 1980*b*. Effects of clear-cutting on gray squirrels. The Journal of Wildlife Management, 44:403–412.

NIXON, C. M., D. M. WORLEY, AND M. W. MCCLAIN. 1968. Food habits of squirrels in southeast Ohio. The Journal of Wildlife Management, 32:294–305.

NOVILLA, M. N., V. FLYGER, E. R. JACOBSON, S. K. DUTTA, AND E. M. SACCHI. 1981. Systemic phycomycosis and multiple fibromas in a gray squirrel (*Sciurus carolinensis*). Journal of Wildlife Diseases, 17:89–95.

PACKARD, R. L. 1956. The tree squirrels of Kansas: ecology and economic importance. Miscellaneous Publications, Museum of Natural History, University of Kansas, 11:1–67.

PARKER, J. C., E. J. RIGGS, AND R. B. HOLLIMAN. 1972. Notes on parasites of gray squirrels from Florida. Quarterly Journal of the Florida Academy of Sciences, 35:161–162.

PASITSCHNIAK-ARTS, M., AND J. F. BENDELL. 1990. Behavioural differences between locally recruiting and dispersing gray squirrels, *Sciurus carolinensis*. Canadian Journal of Zoology, 68: 935–941.

PERRY, H. R., JR., G. B. PARDUE, F. S. BARKALOW, JR., AND R. J. MONROE. 1977. Factors affecting trap responses of the gray squirrel. The Journal of Wildlife Management, 41:135–143.

PHILLIPS, J., AND R. R. DUBIELZIG. 1980. Congenital aortic stenosis in an eastern gray squirrel. Journal of the American Veterinary Medical Association, 177:939.

POCOCK, R. I. 1923. The classification of the Sciuridae. Proceedings of the Zoological Society of London, 1923:209–246.

PRITCHETT, H. D. 1938. Rabies in two gray squirrels. Journal of the American Veterinary Medical Association, 45:563–564.

PURDUE, J. R. 1980. Clinal variation of some mammals during the Holocene in Missouri. Quaternary Research, 13:242–258.

PUDNEY, J., AND D. LACY. 1977. Correlation between ultrastructure and biochemical changes in the testis growth of the American gray squirrel, *Sciurus carolinensis*, during the reproductive cycle. Journal of Reproduction & Fertility, 49:5–16.

REYNOLDS, J. C. 1985*a*. Autumn-winter energetics of holarctic tree squirrels: a review. Mammal Review, 15:137–150.

———. 1985*b*. Details of the geographic replacement of the red squirrel (*Sciurus vulgaris*) by the grey squirrel (*Sciurus carolinensis*). Journal of Animal Ecology, 54:149–162.

RIEGE, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. Journal of Mammalogy, 72:152–162.

ROHER, D. P., M. J. RYAN, S. W. NIELSEN, AND D. E. ROSCOE. 1981. Acute fatal toxoplasmosis in squirrels. Journal of the American Veterinary Medical Association, 179:1099–1101.

SANDERSON, H. R. 1975. Den-tree management for gray squirrels. Wildlife Society Bulletin, 3:125–131.

SCHORGER, A. W. 1949. Squirrels in early Wisconsin. Transactions of the Wisconsin Academy of Science, Arts, and Letters, 39:195–247.

SEEBECK, J. H. 1984. The eastern grey squirrel, *Sciurus carolinensis*, in Victoria. Victorian Naturalist, 101:61–66.

SHARP, W. M. 1959. A commentary on the behavior of free-running gray squirrels. Proceedings of the Southeastern Association Game and Fish Commissioners, 13:382–387.

SHAW, W. W., AND W. R. MANGUN. 1984. Nonconsumptive use of wildlife in the United States. United States Fish and Wildlife Service Resource Publication, 154, 20 pp.

SHIVAPRASAD, H. L., J. P. SUNDBERG, AND R. ELY. 1984. Malignant mixed (carcinosarcoma) mammary tumor in a gray squirrel. Veterinary Pathology, 21:115–117.

SHORT, H. L., AND W. B. DUKE. 1971. Seasonal food consumption and body weights of captive tree squirrels. The Journal of Wildlife Management, 35:435–439.

SHORTEN, M. 1951. Some aspects of the biology of the grey squirrel (*Sciurus carolinensis*) in Great Britain. Proceedings of the Zoological Society of London, 121:427–459.

SIWELA, A. A., AND W. H. TAM. 1984. Ultrastructural changes in the prostrate gland of a seasonally breeding mammal, the grey squirrel (*Sciurus carolinensis* Gmelin). Journal of Anatomy, 138:153–162.

SMALLWOOD, P. D., AND W. D. PETERS. 1986. Grey squirrel food preferences: the effects of tannin and fat concentration. Ecology, 67:168–174.

SMITH, C. C., AND D. FOLLMER. 1972. Food preferences of squirrels. Ecology, 53:82–91.

SMITH, E. N., AND C. JOHNSON. 1984. Fear bradycardia in the eastern fox squirrel, *Sciurus niger*, and eastern grey squirrel, *S. carolinensis*. Comparative Biochemistry and Physiology, A. Comparative Physiology, 78:409–411.

SMITH, N. B., AND F. S. BARKALOW, JR. 1967. Precocious breeding in the gray squirrel. Journal of Mammalogy, 48:328–329.

STAINES, B. W. 1986. The spread of grey squirrels (*Sciurus carolinensis* Gm). Scottish Forestry, 40:190–196.

TAIT, A. J., AND E. JOHNSON. 1982. Spermatogenesis in the grey squirrel (*Sciurus carolinensis*) and changes during sexual regression. Journal of Reproduction & Fertility, 65:53–58.

TAIT, A. J., G. S. POPE, AND E. JOHNSON. 1981. Progesterone concentrations in peripheral plasma of nonpregnant and pregnant grey squirrels (*Sciurus carolinensis*). Journal of Endocrinology, 89:107–116.

TAYLOR, J. C. 1969. Social structure and behaviour in a grey squirrel population. Ph.D. dissert., University of London, London, 217 pp.

———. 1977. The frequency of grey squirrel (*Sciurus carolinensis*) communication by use of scent marking points. Journal of Zoology (London), 183:543–545.

THOMPSON, D. C. 1976. Accidental mortality and cannibalization of a nestling gray squirrel. Canadian Field-Naturalist, 90:52–53.

———. 1977*a*. Reproductive behavior of the grey squirrel. Canadian Journal of Zoology, 55:1176–1184.

———. 1977*b*. Diurnal and seasonal activity of the grey squirrel (*Sciurus carolinensis*). Canadian Journal of Zoology, 55:1185–1189.

———. 1978*a*. Regulation of a northern grey squirrel (*Sciurus carolinensis*) population. Ecology, 59:708–715.

———. 1978*b*. The social system of the grey squirrel. Behaviour, 64:305–328.

THOMPSON, D. C., AND P. S. THOMPSON. 1980 Food habits and caching behavior of urban grey squirrels. Canadian Journal of Zoology, 58:701–710.

THORINGTON, R. W., JR. 1966. The biology of rodent tails: a study of form and function. Arctic Aeromedical Laboratory, Fort Wainwright, Alaska, 137 pp.

———. 1972. Proportions and allometry in the gray squirrel, *Sciurus carolinensis*. Nemouria, 8:1–17.

UHLIG, H. G. 1955. Weights of adult gray squirrels. Journal of Mammalogy, 36:293–296.

VANDER WALL, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, 445 pp.

WALLACH, J. D., AND G. L. HOFF. 1982. Nutritional diseases of mammals. Pp. 127–154, *in* Noninfectious diseases of wildlife (G. L. Hoff and J. W. Davis, eds.). Iowa State University Press, Ames, 174 pp.

WEBLEY, G. E., AND E. JOHNSON. 1982. Effect of ovariectomy on the course of gestation in the grey squirrel (*Sciurus carolinensis*). Journal of Endocrinology, 89:107–116.

———. 1983. Reproductive physiology of the grey squirrel (*Sciurus carolinensis*). Mammal Review, 13:149–154.

WEBLEY, G. E., G. S. POPE, AND E. JOHNSON. 1984. Testosterone, 17-hydroxy-5-androstan-3-one and 4-androstene-3,17-dione in the plasma of male and female grey squirrels. Journal of Steroid Biochemistry, 20:1207–1209.

———. 1985. Seasonal changes in the testes and accessory reproductive organs and seasonal and circadian changes in plasma testosterone concentrations of the male grey squirrel (*Sciurus carolinensis*). General Comparative Endocrinology, 59:15–23.

WEST, R. W., AND J. E. DOWLING. 1975. Anatomical evidence for cone and rod-like receptors in the grey squirrel, ground squirrel, and prairie dog. Journal of Comparative Neurology, 159:439–460.

WHITAKER, J. O., JR., E. J. SPICKA, AND L. L. SCHMELTZ. 1976. Ectoparasites of squirrels of the genus *Sciurus* from Indiana. Proceedings of the Indiana Academy of Science, 85:431–436.

WHITE, F. H., G. L. HOFF, W. J. BIGLER, AND E. BUFF. 1975. A microbiologic study of the urban gray squirrel. Journal of the American Veterinary Medical Association, 167:603–604.

WILD, A. E. 1965. Serum proteins of the grey squirrel (*Sciurus carolinensis*). Immunology, 9:457–466.

———. 1971. Transmission of proteins from mother to conceptus in the grey squirrel (*Sciurus carolinensis*). Immunology, 20:789–797.

WOOD, D. A. 1976. Squirrel collars. Journal of Zoology (London), 180:513–518.

ZIGMAN, S., T. PAXHIA, AND W. WALDRON. 1985. Biochemical features of the grey squirrel lens. Investigative Ophthalmology and Visual Science, 8:1075–1082.

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