Sciurus granatensis. By Leslie Zuhn Nitikman

Sciurus granatensis Humboldt, 1811

Red-tailed Squirrel

Sciurus granatensis Humboldt, 1811:8. Type locality "Carthagène [=Cartagena]," Department of Bolívar, Colombia.

Sciurus variabilis Geoffroy St. Hilaire, I., 1832:classe I. Type locality "la Colombie, plusieurs aux Antilles et quelques-uns aux Etats-Unis." The mounted type bears the legend "Colombie" (Hershkovitz, 1947). Hershkovitz (1947:19) later fixed the type locality as "La Gloria, right bank of the Río Magdalena, about 45 kilometers above the mouth of the Cesar; altitude approximately 45 meters," Department of Magdalena, Colombia.

Sciurus splendidus Gray, 1842:263. Type locality unknown, fixed by Hershkovitz (1947) as "banks of the Río Cesar near its confluence with the Magdalena," Department of Magdalena, Colombia.

Sciurus rufoniger Pucheran, 1845:336. Type locality "la Colombie (Santa-Fé de Bogota)." Later synonymized with *S. g. chrysuros*.

Sciurus chrysuros Pucheran, 1845:337. Type locality "la Colombie (Santa-Fé de Bogota)." Type is an immature form.

Sciurus gerrardi Gray, 1861:92. Type locality "New Granada," fixed by Allen (1915:236) as "Antioqua, Colombia (probably near Medellin)."

Sciurus hyporrhodus Gray, 1867:419. Type locality "Santa Fé de Bogotá," Colombia.

Macroxus griseogena Gray, 1867:429. Type locality was designated as "Venezuela" and later fixed by Hershkovitz (1947: 29) as "San Julián, near La Guaira, coast of Venezuela."

Macroxus xanthotus Gray, 1867:429. Type locality "Costa Rica, Veragua, Cordillera de Tale."

Macroxus tephrogaster Gray, 1867:431. Type locality "Bogotá," Colombia. Alston (1878) later renamed as *S. rufo–niger* (=*S. g. chrysuros*).

Sciurus chapmani J. A. Allen, 1899a:16. Type locality "Caparo, Trinidad."

Sciurus saltuensis J. A. Allen 1899b:213. Type locality "Bonda, Santa Marta District [Department of Magdalena], Colombia," altitude 50 m. Later renamed *S. g. bondae*.

Sciurus versicolor Thomas, 1900:385. Type locality "Cachabi, Prov. Esmeraldas, N. Ecuador. Alt. 160 m," near upper Río Cachaví.

Sciurus nesaeus G. M. Allen, 1902:93. Type locality "El Valle, Margarita Island, Venezuela."

Sciurus tobagensis Osgood, 1910:27. Type locality "Tobago Island, Caribbean Sea."

Sciurus milleri J. A. Allen, 1912:91. Type locality "Cocal (altitude 4,000 ft.)," western Colombia.

Notosciurus rhoadsi J. A. Allen, 1914:585. Type locality "Pagma Forest, Chunchi (altitude 6300 feet), Ecuador." Type specimen is an immature form of *S. g. söderströmi*.

Guerlinguetus griseimembra J. A. Allen, 1914:589. Type locality "Buenavista (altitude 4500 ft.), eastern slope of Eastern Andes, about 50 miles southeast of Bogotá," Department of Cundinamarca, Colombia.

Guerlinguetus candelensis J. A. Allen, 1914:590. Type locality "La Candela (altitude 6500 ft.), near San Agustin, [Dept. of] Huila, Colombia."

Mesosciurus ferminae Cabrera, 1917:49. Type locality "Baeza, (Ecuador oriental)," near Río Mazpa, Napo-Pastaza Province, eastern Ecuador, 1,900 m.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Genus *Sciurus*, Subgenus *Guerlinguetus*. Honacki et al. (1982) recognized eight species within *Guerlinguetus*: *Sciurus aestuans*, *S. gilvigularis*, *S. granatensis*,

S. ignitus, *S. pucheranii*, *S. richmondi*, *S. sanborni*, and *S. stramineus*. Approximately 33 subspecies of *S. granatensis* currently are recognized (Boher, 1981; Cabrera, 1961; Hall, 1981; Handley, 1966), as follows (numbers in parentheses refer to locations of type localities in Fig. 1):

S. g. agricolae Hershkovitz, 1947:16. Type locality "Colonia Agrícola de Caracolicito, Río Ariguaní, on the southern slopes of the Sierra Nevada de Santa Marta, Department of Magdalena, Colombia; altitude 335 meters." (1)

S. g. bondae J. A. Allen, 1899b:213, see above. (2)

S. g. candelensis (J. A. Allen, 1914:590), see above. Misspelled as *candalensis* by numerous authors. (3)

S. g. carchensis Harris and Hershkovitz, 1938:3. Type locality "Atal, about five miles southeast of San Gabriel, Montúfar, Carchi Province, Ecuador, in the cold temperate rain forests of the western slope of the eastern cordillera of the Andes. Altitude about 2900 meters." (4)

S. g. chapmani J. A. Allen, 1899a:16, see above (*quebradensis* J. A. Allen a synonym). (5)

S. g. chiriquensis Bangs, 1902:22. Type locality "Divala," Chiriquí Prov., Panamá, altitude near sea level. (6)

S. g. chrysuros Pucheran, 1845:337, see above (*rufoniger* Pucheran, *hyporrhodus* Gray, and *tephrogaster* are synonyms; misspelled as *chrysurus* by Gray and subsequent authors). (7)

S. g. ferminae (Cabrera, 1917:49), see above. (8)

S. g. gerrardi Gray, 1861:92, see above. (9)

S. g. granatensis Humboldt, 1811:8, see above. (10)

S. g. griseimembra (J. A. Allen, 1914:589), see above. (11)

S. g. griseogena (Gray, 1867:429), see above (*klagesi* Thomas a synonym). (12)

S. g. hoffmanni Peters, 1863:654. Type locality "Costa Rica," later fixed by Harris (1943:9) at "Agua Caliente, San Jose, Costa Rica" (*xanthotus* Gray a synonym). (13)

S. g. imbaburae Harris and Hershkovitz, 1938:1. Type locality "Peñaherrera (Intag) western subtropical part of Imbabura Province, Ecuador; altitude, approximately 1500 meters." (14)

S. g. manavi (J. A. Allen, 1914:589). Type locality "Manavi (Rio del Oro, near sea-level) [Manavi Prov.], Ecuador." (15)

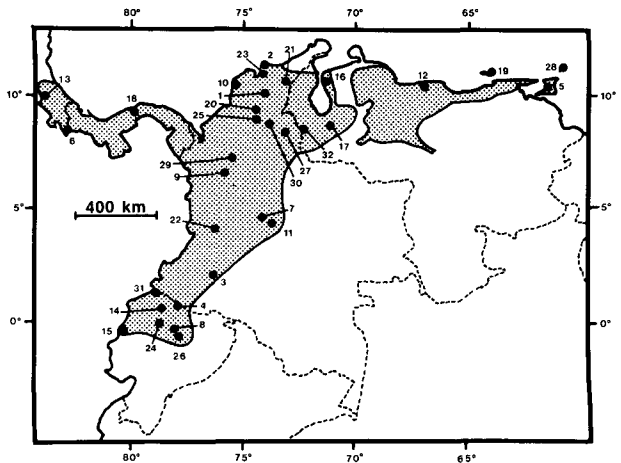*S. g. maracaibensis* Hershkovitz, 1947:25. Type locality "El Pan-

FIG. 1. Geographic distribution of *Sciurus granatensis* in Central and South America. Dots represent the type localities of the 33 subspecies identified in text (see CONTEXT AND CONTENT).

FIG. 2. Adult female *Sciurus granatensis morulus* from Barro Colorado Island, Panamá. Photograph by Carey Thorington.

orama, Río Aurare, a small river emptying into Lake Maracaibo, opposite the city of Maracaibo, Zulia, Venezuela; altitude near sea level." (16)

S. g. meridensis Thomas, 1901:192. Type locality "Escorial, Sierra de Merida. Alt. 2500 m," near Mérida, Venezuela (*tamae* Osgood a synonym). (17)

S. g. morulus Bangs, 1900:43. Type locality "Loma del Leon, Panama," near Gatun (*choco* Goldman, *salaquensis* J. A. Allen, and *baudensis* J. A. Allen are synonyms). Type locality was reduced to a small island by the construction of the Panama Canal (Goldman, 1920). (18)

S. g. neseaus G. M. Allen, 1902:93, see above. (19)

S. g. norosiensis Hershkovitz, 1947:21. Type locality "Norosí, Mompós, Department of Bolívar, Colombia; altitude 120 meters." (20)

S. g. perijae Hershkovitz, 1947:23. Type locality "Sierra Negra, above Villanueva, on the western slope of the Sierra de Perijá, Valledupar, Department of Magdalena, Colombia; altitude 1,265 meters." (21)

S. g. quindianus (J. A. Allen, 1914:587). Type locality "Rio Frio (central Rio Cauca Valley, altitude 3500 feet), western slope of Central (or Quindio) Andes," Department of Valle del Cauca, Colombia (*hyporrhodus* Gray a synonym). (22)

S. g. saltuensis Bangs, 1898:185. Type locality "Pueblo Viejo, Colombia (altitude, 8000 ft.)"; later fixed by Hershkovitz (1947:15) as near "Río San Antonio, northern slope of the Sierra Nevada de Santa Marta, Magdalena, Colombia." (23)

S. g. söderströmi Stone, 1914:14. Type locality "Mount Pichincha." Later fixed by Hershkovitz (1947:37) as "near Quito [Pichincha Prov.], central Ecuador" (*rhoadsi* Allen a synonym). (24)

S. g. splendidus Gray, 1842:263, see above (*magdalenae* J. A. Allen a synonym). (25)

S. g. sumaco (Cabrera, 1917:51). Type locality "San José, al pie del monte Sumaco [Napo-Pastaza Prov.], Ecuador oriental." (26)

S. g. tarrae Hershkovitz, 1947:26. Type locality "Río Tarra, a small tributary of the upper Catatumbo, San Calixto, Department of Norte de Santander, Colombia; altitude about 200 meters." (27)

S. g. tobagensis Osgood, 1910:27, see above. (28)

S. g. valdiviae (J. A. Allen, 1915:309). Type locality "Puerto Valdivia (alt. 360 ft.), lower Rio Cauca," Department of Antioquia, Colombia. (29)

S. g. variabilis Geoffroy St. Hilaire, I., 1832:classe I, see above. (30)

S. g. versicolor Thomas, 1900:385, see above (*inconstans* Osgood, *milleri* J. A. Allen, and *leonis* Lawrence are synonyms). (31)

S. g. zuliae Osgood, 1910:26. Type locality "Orope, Zulia, Venezuela." Later fixed by Hershkovitz (1947:28) as "Orope, a small railroad station on the Río Orope, a tributary of the Zulia, near the Colombian border . . . altitude approximately 25 meters." (*cucutae* J. A. Allen a synonym). (32)

DIAGNOSIS. *Sciurus granatensis* is distinguished from other members of the subgenus *Guerlinguetus* on the basis of the following cranial characteristics: rostrum proportionally longer; angular process larger and more strongly turned inward; cranium more highly arched, whereas maxilla more flattened; external auditory meatus smaller; and basisphenoid and presphenoid flattened ventrally and nearly fused to palatine. In the field, *S. granatensis* may be distinguished from other guerlinguetine squirrels by its bright ochraceous tail and its relatively large size.

GENERAL CHARACTERS. *Sciurus granatensis* is a medium-sized tree squirrel (Fig. 2). Pelage color is so variable that characterization is difficult. Generally, the dorsum is ochraceous, varying from dull yellow sprinkled with black to predominantly black. Some varieties have a black median stripe. The ventrum varies from entirely white to bright orange-rufous. The tail may be deep ochraceous above with a faint sprinkling of black and with or without a pronounced black tip. Ventrally, the tail varies from dark yellowish brown to black edged with ochraceous. The chin and sides of the throat are a fine dusky color with ochraceous highlights. There is an indistinct eye ring of nearly pure ochraceous color. Melanistic individuals have been collected infrequently (Boher, 1981). The skull is rather broad and is depressed in the interorbital region. The brain case is arched and inflated over the interparietal region and is constricted posteriorly. The rostrum and nasals are relatively long and the bullae are small (Fig. 3). *S. granatensis* shows extreme variation in size throughout its range, with no consistent differences between adult males and females (Boher, 1981). Heaney and Thorington (1978) noted a slight mean difference in mass between sexes in the population on Barro Colorado Island, Panamá; females averaged 5.5% larger than males. Throughout the range, body mass ranges from 228 to 520 g (Boher, 1981; Heaney and Thorington, 1978). The ranges of external and cranial measurements of adults (in mm) are: total length, 330 to 520; length of tail, 140 to 280; length of hindfoot, 40 to 65; length of ear, 16 to 36; greatest length of skull, 42.5 to 68.3; condylobasal length, 44.1 to 56.2; zygomatic breadth, 27.0 to 35.7; interorbital width, 15.0 to 24.0; postorbital width, 13.0 to 19.8; mastoid width, 20.0 to 24.0; length of nasal, 14.0 to 20.7; width of nasal, 6.4 to 8.8; palatal length, 22.1 to 27.5; length of maxillary toothrow, 6.4 to 10.7; width of braincase, 20.0 to 25.6; basilar length, 38.0 to 46.0; length of diastema, 11.0 to 15.5; diameter of auditory meatus, 2.95 to 3.75. Measurements are provided by G. M. Allen (1902), J. A. Allen (1899b, 1914, 1915); Bangs (1898), Boher (1981), Goodwin (1946), Harris and Hershkovitz (1938), Hershkovitz (1947), Mendez (1951, 1953), and Osgood (1910, 1912). The dental formula is i 1/1, c 0/0, pm 1/1, m 3/3, total 20 (Mendez, 1951). Enders (1930, 1935) and Mendez (1953) noted three pairs of mammae.

DISTRIBUTION. *Sciurus granatensis* occurs southward from north-central Costa Rica to central Ecuador and eastward from the Pacific Ocean through Venezuela north of the Orinoco River, including the islands of Margarita, Tobago, and Trinidad (Fig. 1).

This species exhibits a wide altitudinal tolerance and has been collected from localities ranging from sea level to 3,000 m (Cabrera, 1961). Handley (1976) noted that in Venezuela, 93% of 178 *S. granatensis* were trapped below 1,500 m; however, he failed to report trapping effort above 1,500 m. *Sciurus granatensis* has no fossil record.

FORM AND FUNCTION. The earliest work concerning *S. granatensis* was a study on the anatomy of the tongue, epiglottis, and larynx (Humboldt, 1811). Humboldt (1811) noted that the larynx was similar to that of *Sciurus erythroeus* Pallas (=*Callosciu-*

rus erythraeus) and different from that of *Sciurus flavus* (=?). Furthermore, he noted that the larynx contained "pockets" similar to those of *Simia oedipus* Brisson (=*Saguinus oedipus*) and of small birds, and was easily confused with *S. oedipus*. He suggested that the structures served as amplification chambers for sound.

Boher (1981) determined that coloration patterns served as diagnostic characters in the identification of Venezuelan subspecies, although Hershkovitz (1947) found that color variation among the squirrels of northern Colombia was related in part to environmental changes within and among localities. During the rainy season (October to November), the pelage is reddish. During the dry season (May to June), a second molt occurs, resulting in a new orange-colored pelage (Hershkovitz, 1947). Intermediate coloration may be the result of specimens being collected during the molt. In the tropical lowlands, the pelage is short and coarse, often with no underfur, whereas at higher elevations, the pelage is thick and wooly (Allen, 1915; Goldman, 1920).

The baculum is small in proportion to the penis. The bone is thick, with a flattened distal spur (Boher, 1981). A small accessory spur lies anterior to the main one (Burt, 1960). The posterodorsal part of the baculum is "sharply pointed and a notch is formed with the shaft, which has a dorsal keel" (Burt, 1960:33). The basal portion is much reduced (Boher, 1981). The ranges of penis measurements (in mm) are: length, 8.5 to 11.0; proximal width, 2.5 to 3.5; distal width, 2.5 to 3.5; smallest width, 1.0 to 1.5 (Burt, 1960; Didier, 1955). Burt (1960) noted that the morphology of the baculum suggested a relationship with *S. deppei* and *S. negligens* (=*S. deppei negligens*). Layne (1954:364) noted that a single os clitoridis of *S. gerrardi* (=*S. g. gerrardi*) was similar to that of *S. carolinensis* but differed in that it had a relatively larger distal expansion, "a less distinct ventral projection, and no well-developed ridge on the convex surface of the disc." The specimen he examined measured 4.2 mm in length and 2.0 mm at the greatest width. Burt (1960) recorded a 3.7-mm specimen.

Average brain mass was recorded as 6.5 g (Mace et al., 1981).

Sciurus granatensis in the lowlands of central Panamá exhibits a high degree of dietary specialization on the hardest-shelled nuts in the forest, but no studies have been done on the jaw structure enabling this specialization (Glanz, 1984).

ONTOGENY AND REPRODUCTION. The gestation period was reported as less than 2 months (Méndez, 1970), but its precise length is not known. Heaney and Thorington (1978) assumed the length of gestation was approximately 44 days, similar to that of *Sciurus carolinensis*. Glanz et al. (1982) observed that gestation and lactation lasted 15 to 16 weeks, also comparable to temperate species.

Young are born hairless and with closed eyes. A pair born to a captive female weighed 9 and 10 g at birth (Boher, 1981). Boher (1981) examined five pregnant females; two were carrying two embryos each, whereas three had three embryos. Enders (1935) reported that the usual number of embryos for *S. granatensis* on Barro Colorado Island (BCI) was two; he found only one female to carry three embryos. Pirlot (1963) found one and two embryos in two pregnant females from western Venezuela. Handley (cited in Emmons, 1979) reported that the mean size of four litters was 1.8. Glanz et al. (1982) noted that the mean size of weaned litters on BCI was 1.9 (*n* = 12).

On BCI, breeding activity usually begins with the onset of the dry season in late December and early January (Heaney and Thorington, 1978). Lactating females were seen in late May and June, indicating a second litter at this time of the year (Heaney and Thorington, 1978). Mating bouts during June and July suggested a third litter possibly was produced by some females (Heaney and Thorington, 1978). Enders (1935) reported that all of the adult males and females collected in June showed evidence of breeding activity. A female was collected in late June with embryos 15 cm long and a pair of half grown young was seen in late July (Enders, 1930). Glanz et al. (1982) noted that mating activity in the dry season was roughly synchronous, with nearly all adult females becoming estrous in December and January. Subsequent litters seemed less synchronous. Glanz et al. (1982) observed that the period of mating activity from December to August corresponded to the availability of the four dominant food species. Conversely, no mating activity was observed from September through November, when fresh fruits were scarce and squirrels became dependent upon cached nuts and other less-used foods. Resumption of mating activity in
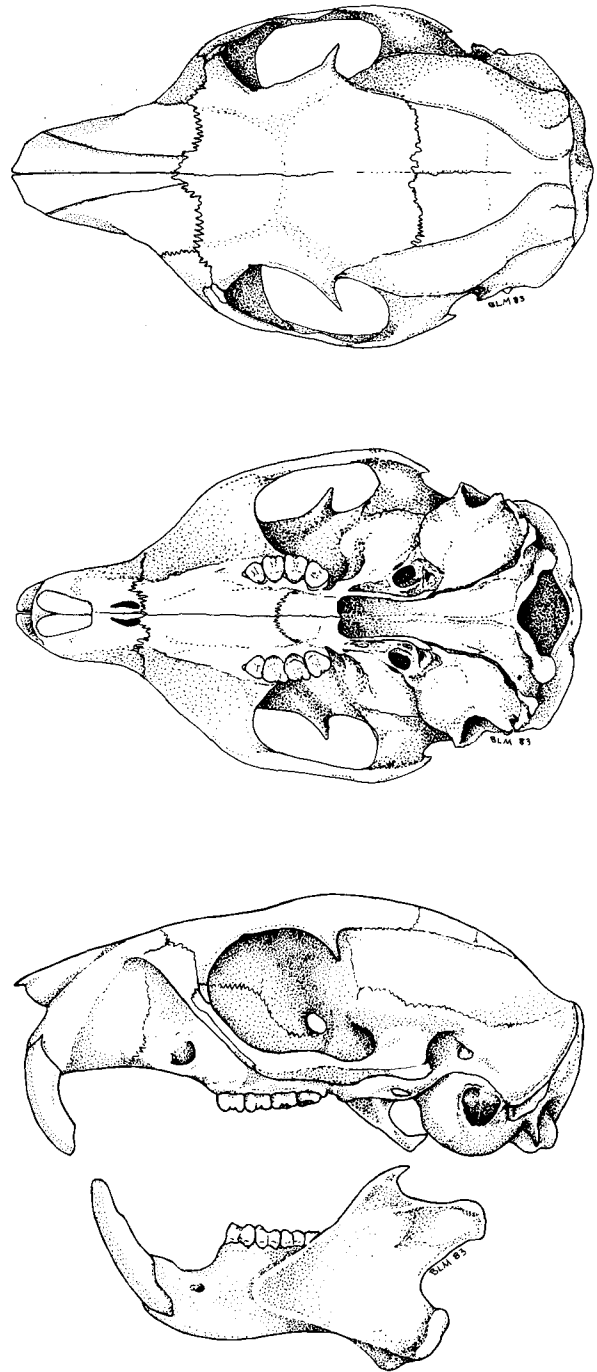

FIG. 3. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a female *Sciurus granatensis morulus*. Specimen collected in the Panama Canal area and housed in a private collection. Illustrations by Bettina L. McLeod. Greatest length of skull is 56 mm.

December coincided with the massive fruiting of *Dipteryx panamensis* (Glanz et al., 1982). Litters conceived in the dry season of 1977 were more likely to survive than those conceived later in the year (Glanz et al., 1982). Eight young from seven dry-season litters survived to be trapped, whereas later in the year, only three survived from eight litters. Litters born when *Dipteryx* fruited evidently grew faster than later litters. Between 1976 and 1979, females on BCI produced an average of 3.8 young per year (Glanz et al., 1982). Testes of adult males remained scrotal throughout the year, but were more densely haired in December and probably November (Heaney and Thorington, 1978).

At Rodman Naval Ammunition Depot, a dry tropical forest

area on the Pacific Coast near Balboa, Panamá, chases involving groups of six to eight individuals were observed on 12 August 1966, 1 November 1966, 31 January 1967, 4 and 7 April 1967 (Fleming, 1970). At Fort Sherman Military Reservation, a wet tropical habitat on the Atlantic Coast, Fleming (1970) observed a similar chase on 11 April 1967. Pregnant females were collected in Venezuela on 16 September 1963, 6 March 1966, 25 September 1968, 11 October 1969, and 18 September 1980 (Boher, 1981). At San Julián, Venezuela, mating chases were seen in late July and early August (Robinson and Lyon, 1902).

Little is known about the longevity of *S. granatensis*. One adult female on BCI was marked when at least 1 year of age and was recaptured repeatedly over the next 6 years (J. R. Giacalone-Madden, in litt.).

ECOLOGY. Throughout its range, *S. granatensis* occurs in a diversity of habitats, from tropical forests, where populations reach high densities, to croplands, where it is considered a serious pest. On BCI, *S. granatensis* was seen most frequently in second growth forest adjacent to mature forest (Enders, 1935). Enders (1935) rarely observed squirrels in suitable habitat off the island and presumed this was because of local hunting pressure. Handley (1976) collected throughout Venezuela and found that 73% of the squirrels were trapped near water, 62% in evergreen forests, 27% in dry areas, 7% in cloud forests, and 1% each in deciduous forests and thorn forests. Twenty-nine percent of the squirrels were caught in human-altered habitats, such as cleared areas, orchards, and pastures. Handley (1976) did not state if trapping effort was distributed evenly throughout all habitat types. At Parque Nacional Guatopo, Venezuela, *S. granatensis* was seen most frequently in dry habitat with mixed canopy cover and dense understory (August, 1981).

On BCI, activity begins shortly after sunrise (0630 h). Individuals forage until approximately 1100 h, after which they generally are inactive until approximately 1530, when they forage again until sunset (1730 h; Bonaccorso et al., 1980).

Sciurus granatensis is common both on the ground and in trees. On BCI, most activity occurred less than 15 m above the ground (Heaney and Thorington, 1978). However, when *Dipteryx* was fruiting, squirrels frequently were observed to feed in the crown, often 30 m above the forest floor. At Rodman, Panamá, *S. granatensis* was observed on the ground only 2.6% of the time (Garber and Sussman, 1984). Squirrels were seen to travel primarily in the upper two-thirds of the forest strata. They most frequently used trunks and thick branches. In trapping throughout Venezuela, Handley (1976) caught *S. granatensis* on the ground only 1% of the time. In Bush Bush Forest, Trinidad, a swamp forest, *S. granatensis* commonly was observed but was never caught in traps set only on the ground (Worth et al., 1968). In the dense forest of the Paramo de Tama, Colombia, squirrels were seen almost exclusively high in the forest canopy (Osgood, 1912). Lianas and vines were used as aerial highways and squirrels leaped long distances when necessary (Enders, 1935).

Heaney and Thorington (1978) estimated the minimum home range area of males on BCI to be 1.49 ha (range 0.83 to 2.15 ha). The minimum home range area for adult females (size calculated from observations of marked individuals) was 0.64 ha (range 0.39 to 0.86 ha; Heaney and Thorington, 1978). Using radio-telemetry, Giacalone-Madden (in litt.) found that home ranges of females were larger than those of males (range 2 to 4 ha for females). Ranges for females were considered essentially non-overlapping. Adult females were never seen closer together than 10 m without exhibiting threat displays; occasionally physical attacks occurred. Adult females generally did not feed in the same tree at the same time unless it was a large tree. Home ranges of adult females always included at least one fruit-producing *Scheelea*, *Dipteryx*, or cluster of *Gustavia* and several nesting trees. In contrast, home ranges of adult males overlapped extensively with those of other males and females; males often congregated at locally abundant food sources or around an estrous female. Subadults remained near the nest until weaned (Heaney and Thorington, 1978). When weaned, they remained within the maternal home range for several more weeks before dispersing. Adult males moved an average of 162 m before being recaptured, whereas adult females moved 62 m and subadults moved only 35 m (August, 1981). Within a population at Guatopo, Venezuela, there was no difference between breeding and non-breeding females in the distance moved along a 1.7-km transect, suggesting that adult females maintained the same territories throughout the year (August, 1981).

Squirrel populations attained greatest density along tops and sides of ridges vegetated with many palms (Chapman, 1938); lowest densities were recorded in ravine bottoms (Fleming, 1970). Eisenberg and Thorington (1973) estimated from censuses that BCI supported 300 individuals (a mean density of 0.2 squirrels/ha). Heaney and Thorington (1978) later estimated the squirrel density on BCI to be 2.5 squirrels/ha for the entire study site, whereas optimal habitat was able to support 5 squirrels/ha. The discrepancy may be partly related to an initial underestimation by Eisenberg and Thorington (1973), but seemingly the number of squirrels observed in the intervening years has increased (Heaney and Thorington, 1978). More recently, Glanz (1982b) estimated the squirrel population on BCI to be 2,700 individuals. On a 10-ha study area, Glanz et al. (1982) found 2.1 squirrels/ha in January, 3.2/ha in July, 2.3/ha in November 1977, and 1.9/ha in July 1979. These estimates of density, based on mark-resighting indices, generally show an increase during the breeding season and a decline in November when principal foods are scarce. Glanz et al. (1982) noted that in the intervening years, there were two consecutive crop failures of *Dipteryx* and *Gustavia*. He attributed the decrease in squirrel abundance to stress-related low reproductive success. By use of a 4-ha grid configuration of live-traps, O'Connell (1981; 1982) estimated the mean density of squirrels at 0.33/ha at Masaguaral, Venezuela. August (1981) censused a population at Guatopo, Venezuela, along a 1.7-km line transect and reported a density of squirrels of 0.13/ha. A density of 25/km² (0.25/ha) was estimated for Guatopo by Eisenberg et al. (1978) and Eisenberg (1980). Based on mark-recapture studies, Eisenberg et al. (1978) estimated the density of squirrels at Masaguaral to be 40/km² (0.4/ha) in deciduous forest and 50/km² (0.5/ha) in moderately flooded lowlands.

Annual survivorship of squirrels on BCI was estimated to be between 50% and 64% over 3 years (Glanz et al., 1982). Eleven individuals disappeared from a marked population of 45 between January 1977 and June 1979. Of these, five were last observed during the season of food scarcity. Glanz et al. (1982) attributed most of these disappearances to mortality rather than to dispersal because none reappeared in other parts of the forest. Infant mortality seemed high in this population, as more than half of the litters disappeared before leaving the nest. O'Connell (1982) reported a high rate of survival among squirrels of the seasonally flooded llanos of Venezuela.

Heaney and Thorington (1978) found that in June 1976, the population was composed of 72% adults and 28% subadults. The following month, when the second litter of the year was weaned, adults accounted for 44% of the population, whereas subadults represented 56% of the population. In December 1976, 59% were adults and 41% were subadults. The ratio of males to females was about equal on BCI (Heaney and Thorington, 1978).

Known predators of *S. granatensis* include *Cebus* monkeys, and other arboreal carnivorous mammals, raptors, boa constrictors (*Constrictor constrictor*) and other arboreal snakes (Enders, 1935; Méndez, 1970). Oppenheimer (1968, 1982) reported *Cebus* eating two infant squirrels on BCI. The monkey peeled off and ate only the gray pigmented skin; when the squirrels were nearly skinned, their bodies were dropped. Both were already dead when the monkey first was observed to feed on them; they probably were removed from the nest. Glanz (in litt.) observed five instances of raptors diving at *S. granatensis*; the birds were three ornate hawk-eagles (*Spizaetus ornatus*), one subadult white eagle (*Leucopternis albicollis*), and one gray-headed kite (*Leptodon cayanensis*). None of the attacks was successful but they provoked vigorous alarm calls by the squirrels. Throughout its range, *S. granatensis* is hunted by humans for food. Hernández-Camacho (1957) reported that the flesh is highly prized by the residents of the Department of Santander, Colombia.

Sciurus granatensis was tested as a potential reservoir host of leishmaniasis (Herrer et al., 1973), St. Louis encephalitis (Seymour et al., 1983), yellow fever (Seymour et al., 1983), Ilhéus virus (Rodaniche and Galindo, 1963; Seymour et al., 1983), Mayaro virus (Seymour et al., 1983), and echinococcus infection (D'Alessandro et al., 1981). No infected squirrels were found in these studies. Clark and Dunn (1932) reported an instance in Panamá of a pet squirrel infected with Chagas' disease being kept in a house where two children also were infected. Arcay (1981) described two coccidian parasites, *Eimeria guerlingueti* and *Wenyonella maligna*, removed from the intestinal tract of Venezuelan squirrels.

Ectoparasites recorded from *S. granatensis* include 19 species of Acarina: *Acanthonyssus proechimys* (Saunders, 1975), *Am-*

blyomma longirostre (Jones et al., 1972), *Amblyomma* sp. (Fairchild et al., 1966; Jones et al., 1972), *Androlaelaps fahrenholzi* (Furman, 1972), *Crotiscus* sp., *C. desdentatus* (Brennan and Reed, 1975*b*), *Eutrombicula alfreddugesi* (Brennan and Yunker, 1966), *E. goeldii* (Brennan and Reed, 1975*b*; Brennan and Yunker, 1966), *E. tropica* (Brennan and Reed, 1975*a*), *Haemolaelaps glasgowi* (Furman, 1972; Tipton et al., 1966; Wenzel and Tipton, 1966), *Hirstionyssus keenani* (Herrin and Yunker, 1975; Yunker and Radovsky, 1966), *Ixodes* sp. (Fairchild et al., 1966), *I. tiptoni* (Fairchild et al., 1966; Wenzel and Tipton, 1966), *Odontacarus sunnianae* (Brennan and Reed, 1975*a*, 1975*b*; Brennan and Yunker, 1966), *O. tubercularis* (Brennan and Reed, 1975*a*, 1975*b*), *Trombicula dicrura*, *T. dunnii*, *T. keenani*, and *T. manueli* (Brennan and Yunker, 1966). Also, seven species of Anoplura were collected from the species: *Enderleinellus* sp. (Wenzel and Johnson, 1972), *E. insularis*, *E. venezuelae*, *Hoplopleura sciuricola* (Ferris, 1951; Johnson, 1972), *Neohaematopinus* sp. (Wenzel and Johnson, 1966), *N. sciurinus* (Ferris, 1951), and *N. semifasciatus* (Johnson, 1972). Fleas (Siphonaptera) recorded from *S. granatensis* include: *Dasypsyllus gallinulae* (Tipton and Machado-Allison, 1972; Tipton and Méndez, 1966), *Juxtapulex echidnophagoides* (Tipton and Méndez, 1966), *Kohlsia graphis* (Tipton and Méndez, 1966; Wenzel and Tipton, 1966), *K. tiptoni*, *K. traubi* (Tipton and Méndez, 1966), *Neotyphloceras rosenbergi* (Johnson, 1957; Méndez, 1977), *Orchopeas howardi* (Tipton and Machado-Allison, 1972), *Pleochaetis dolens* (Jordan and Rothchild, 1914; Tipton and Machado-Allison, 1972; Tipton and Méndez, 1966; Wenzel and Tipton, 1966), *Polygenis bohlsi* (Johnson, 1957; Tipton and Machado-Allison, 1972), *P. dunni* (Tipton and Machado-Allison, 1972; Tipton and Méndez, 1966; Wenzel and Tipton, 1966), *P. klagesi* (Johnson, 1957; Tipton and Machado-Allison, 1972); *P. occidental* (Tipton and Machado-Allison, 1972), *P. roberti* (Tipton and Méndez, 1966; Wenzel and Tipton, 1966), *Rhopalopsyllus* sp., *R. australis* (Tipton and Méndez, 1966), *R. steganus* (Fox, 1947), and *Strepsylla dalmati* (Tipton and Méndez, 1966).

Studies on BCI show that *S. granatensis* has a high degree of dietary specialization for hard-shelled nuts (Bonaccorso et al., 1980; Glanz, 1982*a*; Glanz et al., 1982; Heaney and Thorington, 1978). Observations in Costa Rica, however, suggest that squirrels are "opportunists who consume almost anything that will yield a little nourishment" (Skutch, 1980:83). On BCI, *S. granatensis* was observed to feed on 58 species of native plants (Glanz et al., 1982). On rare occasions, individuals fed on fungi (Boher, 1981; Glanz et al., 1982; Heaney and Thorington, 1978; Méndez 1970) and tree gums (Garber and Sussman, 1984; Hershkovitz, 1977). In northern Venezuela, squirrels were seen to chew on bases of bromeliads (O'Connell, 1981). In areas of human habitation, the species is known to feed heavily on cultivars, such as mangos, guavas, avocados, coconuts, maize, cacao, bananas, and the various species planted to shade coffee crops (Boher, 1981; Heaney and Thorington, 1978; Hernández-Camacho, 1957; Mendez, 1951; Osgood, 1912; Robinson and Lyon, 1902; Skutch, 1971, 1980; Vesey-FitzGerald, 1936). The damage caused to these crops by squirrels is considered substantial. Vesey-FitzGerald (1936) noted that on Trinidad it was an established practice to pay a bounty of $0.06 for each squirrel tail. In the Department of Santander, Colombia, the bounty was $1.50 per tail (Hernández-Camacho, 1957).

Sciurus granatensis also is known to feed occasionally on animal material. In Costa Rica, Skutch (1980) observed a squirrel to tear away at a large decaying vine to reach insect larvae within. Glanz et al. (1982) saw squirrels feed on insects and frog eggs, but these accounted for only about 0.4% of all feeding bouts, although some of their 43 observations of bark feeding could have involved insect larvae. The low level of insect consumption is noteworthy because insects are a significant food source for many other tropical sciurids (Emmons, 1980; Medway, 1969). Skutch (1980) attributed a proportion of the mortality of bird eggs and nestlings to predation by squirrels.

Despite the large number of plant species eaten by squirrels on BCI, feeding observations indicated that four species, *Astrocaryum standleyanum*, *Dipteryx panamensis*, *Scheelea zonensis*, and *Gustavia superba*, were eaten 73% of the time (Glanz et al., 1982). The first three species have hard woody nuts covered by a sugary or oily exocarp. Only three mammal species are known to be able to crack the hard shell and feed on the inner seed; these are *Sciurus granatensis*, *Dasyprocta punctata* (agouti), and *Tayassu tajacu* (collared peccary), all comprising what Glanz (1982*a*) referred to as the "hard-nut eating guild." Only squirrels have both arboreal

and terrestrial access to ripe fruits. When fruit is taken from the ground, the squirrel usually returns to a perch several meters above the ground before eating (Heaney and Thorington, 1978). The feeding perch is usually horizontal in orientation and between 3 and 8 cm in diameter (Garber and Sussman, 1984). Squirrels usually eat only the seeds of *Astrocaryum*, *Dipteryx*, and *Scheelea*, and often discard the fruit with much seed material remaining. Agoutis seem to "prefer fruits opened by squirrels and consequently are attracted to trees where squirrels are feeding" (Bonaccorso et al., 1980:66). I observed squirrels to spend 40 min to gnaw through the hard shell; Bradford and Smith (1977) and Bonaccorso et al. (1980) made similar observations.

When the massive *Dipteryx* fruit crop ripens in December and January on BCI, it accounts for up to 80% of the feeding bouts (Glanz et al., 1982). Similarly, when the other three commonly used food species are in season, *S. granatensis* feeds on them heavily (Bradford and Smith, 1977; Glanz et al., 1982). From September through November, none of the principal fruits are available and squirrels must rely on cached nuts, primarily *Scheelea* palms, and on various fleshy, small-seeded fruits such as *Coccoloba*, *Eugenia*, *Protium*, and *Spondias* (Glanz et al., 1982). This season is a time of stress for squirrels, evidenced by weight loss, greater mortality, and a greater trapping success (Glanz et al., 1982).

Palm nuts composed 76% of the diet of *S. granatensis* in the dry forest habitat of Paraiso, Panamá (Glanz, 1982*a*, 1984). In contrast, *S. variegatoides*, a sympatric squirrel, was observed to feed on palm fruit only 4% of the time and in each instance fed only on the mesocarp, discarding the intact nut (Glanz, 1984). At sites where *S. granatensis* was absent, *S. variegatoides* seems to be the main rodent consumer of palm nuts (Bradford and Smith, 1977). At the Rodman site, where the two species are sympatric, Fleming (1970) saw both carrying hard palm fruits. *Scheelea zonensis* was the fruit most frequently eaten at this location (Garber and Sussman, 1984). Other major foods were *Dipteryx panamensis*, *Gustavia superba*, and *Maripa panamensis*. In the Department of Santander, Colombia, squirrels fed primarily on the fruits of two palms, *Phytelephas* and *Attalea* (Hernández-Camacho, 1957). In northern Venezuela, squirrels were observed to feed on the fruits of *Ficus*, *Persea*, and *Spondias* (O'Connell, 1981).

The diet of *S. granatensis* in central Panamá is composed primarily of nuts that few other mammal species can use; hence, few competitive interactions are likely (Glanz, 1984). Were it not for the staggered availability of its three principal nuts on BCI, *S. granatensis* might face greater interspecific competitive pressures, might have a shorter and less productive breeding season, and be less abundant (Glanz, 1984). At Paraiso, competition with *S. variegatoides* may occur. At Rodman, competition with the "squirrel-like" *Saguinus oedipus* was not evident (Garber and Sussman, 1984). In Antioquia, Colombia, Hershkovitz (1977) observed that *S. granatensis* chased away the smaller *Sciurus pucherani* whenever the latter attempted to feed on sap from the same tree. In this highland locality, palms are scarce; specialization on palm nuts is unlikely.

Heaney and Thorington (1978) observed that age and sex classes may have different food habits. Between 15 December 1976 and 15 January 1977, they observed adult males to eat three species of plants, but adult females ate four species and subadults ate eight species. Nearly all flowers, bark, and leaves consumed by squirrels were eaten by adult females and subadults. *Dipteryx* accounted for 80% of the diet of adult males, but only 46% of that of adult females and 54% of that of subadults. Glanz et al. (1982) found that fungi and animal material were eaten primarily by subadults and reproductive females; they suggested that these foods might be supplying specific nutrients.

Sciurus granatensis is considered not only a major consumer of hard fruits but also the principal disperser as well (Bonaccorso et al., 1980; Enders, 1930). Bonaccorso et al. (1980) reported that on numerous occasions squirrels carried fruit well beyond the crown of the parent tree before feeding. Squirrels carried nuts an average of 13.9 m from the parent tree when scatter-caching (Heaney and Thorington, 1978). Smith (1975) suggested that scatter-caching behavior reduced the chance of nuts being attacked by beetles of the family Bruchidae.

BEHAVIOR. *Sciurus granatensis* usually is solitary and is seen in groups only during the breeding season, at feeding aggregations, or when with young. Heaney and Thorington (1978) noted that even in seemingly tight feeding aggregations, the squirrels

maintained spatial distances of several meters and actively avoided each other. Social interactions between a female and her young were limited to attempts by the young to nurse and to occasional short bouts of wrestling.

Garber and Sussman (1984) reported that sitting occupied 64% of their daily activity whereas activities such as grasping, jumping, and climbing only totaled 3%.

Sciurus granatensis was observed in interspecific association with mixed bird flocks in western Panamá and northern Andes (Moynihan, 1962; 1979), and with rufous-naped tamarins (*Saguinus geoffroyi*) and squirrel monkeys (*Saimiri sciureus*) in western Panamá (Moynihan, 1976). Moynihan (1979) noted that squirrels usually were silent when associating with bird flocks. An avoidance mechanism seemed to operate between squirrels and tamarins in central Panamá (Moynihan, 1976); on the rare occasions they were observed together, the squirrels showed obvious hostility.

Squirrels at times seem indifferent to human observers, but at other times they are shy and quick to run off if disturbed (Bonaccorso et al., 1980; Enders, 1935; Goldman, 1920; Osgood, 1912). My own observations suggest that the indifferent individuals may be residents, whereas the shy nervous ones are transients.

Sciurus granatensis usually is silent; nevertheless, it has several distinctive calls. When alarmed, squirrels emit a few short, rather hoarse notes. Bold individuals vocalized at human observers when disturbed, in a manner similar to that of *Tamiasciurus hudsonicus* (Enders, 1930; 1935). During mating chases, squirrels were observed to grunt, chuck, and squeal (Fleming, 1970).

Mating behavior is similar to that of other sciurids. Males were attentive to females three or more days preceding estrus (Heaney and Thorington, 1978). On the morning a female became estrous, many males congregated within her home range, followed her closely, and chased each other (Glanz et al., 1982). Chasing sometimes continues for many hours with a gradual increase in excitement before a successful mounting occurs. In most instances, there is a single brief copulation (approximately 10 s). Males usually lose interest in the female within 15 to 30 min following a successful mounting.

Females transport young by grabbing them by the underside or flank with their incisors; the infant's limbs hug the female's neck, and its tail curls over her shoulders and back (Lang, 1925).

Enders (1930) observed a squirrel to hold a fruit in its forepaws and, with a movement of the head up and backwards and of the paws down and forwards, tear off the husk in several pieces with its incisors. With the husk removed, the squirrel proceeded to eat the soft exocarp surrounding the nut, rotating it in its forepaws until only the nut remained. The squirrel then dropped the intact nut. Other workers noted that squirrels only ate the seeds of fruits and scraped away and discarded the sweet exocarp to expose the nut. They were observed to "gnaw small flakes to gradually open a hole through which they . . . [could] scrape out seed material with their incisors" (Bradford and Smith, 1977:672).

In Costa Rica, Skutch (1980) observed squirrels to cache nuts of *Calatola costaricensis* and *Clusia* sp. On BCI, squirrels were seen to cache many food species, primarily *Astrocaryum, Gustavia,* and *Scheelea* nuts (Heaney and Thorington, 1978). Cached nuts had nearly all of the pulpy exocarp removed first. Squirrels cached food on the ground and in trees with equal frequency (Heaney and Thorington, 1978). Arboreal caches were located 1 to 12 m above the ground, with a mean height of 5 m. Each food item was cached separately (scatter-caching). Fruit was cached most frequently atop a liana or branch fork. Arboreal caches always disappeared within 24 h (Heaney and Thorington, 1978). *Scheelea* was the nut cached most frequently on the ground and also was the only species they observed squirrels to recover and eat at a later date. Terrestrial caches nearly always were at the base of a tree, against a buttress, or beside a liana where it lay on the ground. Terrestrial caching was seen most commonly from May through August and rarely was seen in December and January during *Dipteryx* fruiting and immediately after the seasonal food scarcity. Cached palm nuts formed 3% of the diet in July 1977, but rose to 20% of all feeding sessions in late November (Glanz et al., 1982).

Radio-tracking studies indicate that *S. granatensis* has a precise spatial memory of its home range. Giacalone-Madden (in litt.) observed that squirrels often took a direct route to distant trees to ascertain the ripeness of fruit or to recover cached fruit hidden months earlier.

Skutch (1980) observed a squirrel to bite off slender twigs and

moderate-sized leaves, fold the twigs in half in its mouth, and carry them into a vine tangle. The squirrel made many such trips without stopping. When the outer walls of the nest were complete, the squirrel gathered mouthfuls of "soft, fibrous inner bark" to line the inside.

GENETICS. Nadler and Hoffmann (1970) reported a diploid number of 42 chromosomes and a fundamental number of 78 chromosomal arms from a male of unknown origin and a female from Monte Avila, Los Venados, Venezuela. The karyotypes showed 19 pairs of metacentric and submetacentric autosomes, a single pair of acrocentric autosomes, a large submetacentric X- and a medium-sized submetacentric Y-chromosome. Comparison with other *Sciurus* species showed that *S. granatensis* was chromosomally divergent. Nadler and Hoffmann (1970) theorized that chromosomal fissioning resulted in the diploid number being higher than among most sciurids. These findings support the "accepted opinion that South American sciurids evolved from ancestral North American stock" (Nadler and Hoffmann, 1970:1385).

REMARKS. Jones and Genoways (1971, 1975) noted an overall similarity between *S. granatensis* and *S. richmondi*, a squirrel found within the borders of Nicaragua, and suggested that the two might be a single species. They were reluctant to lump them because of what they considered a significant size difference. However, external and cranial measurements of *S. richmondi* (Jones and Genoways, 1971) generally fall within the known ranges for *S. granatensis*. A male collected at Cataratas, San Carlos, Costa Rica (AMNH 141922), possibly is an intergrade between the two taxa; it possessed characteristics of both (Jones and Genoways, 1971).

The specific name *granatensis* means "from Granada," in reference to the type locality in New Granada, an area now encompassing modern-day Colombia and Venezuela.

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