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COMPARATIVE NATURAL HISTORY OF SMALL MAMMALS FROM TROPICAL FORESTS IN WESTERN MEXICO

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Neotropical forest ecosystems are biologically diverse and are disappearing at high rates. Neotropical deciduous forests, found on the Pacific coast of North America from Mexico to Panama, have been highly fragmented and are threatened with total destruction (Janzen, 1988). The ecology of small mammals of these forests is poorly known, but observations on spiny pocket mice (*Liomys*) and other heteromyid and cricetid rodents in Costa Rica and Panama suggest that these mammals play a key role as seed predators (Fleming, 1974; Janzen, 1983). The mammalian fauna of Mexican deciduous forests is diverse and exhibits high endemism (Ceballos and Navarro, in press). I review herein the natural history of seven species of small mammals inhabiting a deciduous forest and adjacent habitats at Chamela, Jalisco, Mexico. Detailed information about their population and community ecology is presented elsewhere (Ceballos, 1989).

Field work was conducted from April 1986 to June 1987. Most observations were made at the 1,600-ha Chamela Biological Station (19°30'N, 105°03'W) located in the state of Jalisco, about 125 km NW Manzanillo. Additional, but less intensive, observations were made in nearby habitats not represented in the station. Elevation ranges from 20 to 500 m, and the topography consists primarily of low hills separated by seasonal watercourses. The climate is characterized by pronounced dry-wet seasonality. The average monthly temperature is 24.9°C, and mean annual precipitation is 748 mm, with 80% falling from July to October (Bullock, 1986). At the Chamela Biological Station, tropical deciduous forest predominates on the hillsides and semideciduous forest (arroyo forest) along the watercourses. Nearby vegetation types are grassland, thorn forest, mangrove, palm forest, riparian forest, and crops (Ceballos and Miranda, 1986).

In the deciduous and arroyo forests, small mammals were live-trapped by use of 64 Sherman traps set in each of three 0.5 ha grids per habitat. Traps were set 3 consecutive nights each lunar month during the new moon. Arboreal species were sampled by placing an additional 16–18 Sherman traps on wood platforms in trees (Table 1). Traps were baited with a mixture of rolled oats, peanut butter, and vanilla extract. Trapping in other habitats (mangrove, riparian forest, thorn forest, palm forest, grassland, and crops) was conducted using similar techniques, but each of these habitats was sampled on only one grid three times throughout the year. Densities were estimated by direct count to determine the minimum number of individuals known to be alive (Krebs, 1966).

For each individual captured, external measurements (length of hind foot in mm, and mass in g) and reproductive condition (for females, nonreproductive, presence of palpable embryos, or lactating; for males,

testes abdominal or scrotal) were recorded. A few individuals of all species except *Reithrodontomys fulvescens* and *Sigmodon mascotensis* were kept in the laboratory to study diet and reproduction.

Eleven species of small mammals (*Baiomys musculus, Liomys pictus, Marmosa canescens, Nyctomys sumichrasti, Oryzomys couesi, Oryzomys melanotis, Osgoodomys banderanus, Peromyscus perfulvus, Reithrodontomys fulvescens, Sigmodon mascotensis,* and *Xenomys nelsoni*) were captured. One species, *Sciurus colliaei,* was seen but not captured, and two additional species, *Hodomys alleni* and *Pappogeomys bulleri,* previously recorded in the area (Ceballos and Miranda, 1986) were not seen. Of the mammals known from the Chamela Biological Station, three genera (23%) and nine species (64%) are endemic to Mexico.

The number of species per habitat ranged from one to nine. The most abundant species overall was the spiny pocket mouse (*Liomys pictus*). In the deciduous and arroyo forests (the most intensively sampled habitats) it accounted for 95% (302) and 71% (251) of all individuals captured, respectively. All species except *Sigmodon mascotensis* and *Sciurus colliaei* were nocturnal, and most (71%) were herbivorous.

Marmosa canescens.—The grayish mouse opossum is endemic to Mexico (Hall, 1981). It is solitary and semiarboreal (six of 11 captures were on the ground). It was present in all forest habitats and croplands, but not in grassland. Nests are made of dry leaves and are lined with grasses and plant fibers. The nests (n = 25) were found in cavities in trees and shrubs, such as *Caesalpinia eriostachys, Jacquinia pungens, Opuntia excelsa,* and *Prosopis juliflora,* at heights from 70 to 500 cm; only one was found on the ground beneath a pile of brush. Ten nests were found in abandoned nests of the white-bellied wren (*Uropsila leucogastra*—L. Marquez, pers. comm.). Estimated densities of *M. canescens* in both deciduous and arroyo forests ranged from 0.4 to 4.5 individuals per ha. Females with young were found from July to September, and males with scrotal testes from January to August. Juveniles were collected in February, March, April, June, and July. Number of young in three litters was 8, 13, and 14, and dispersal from the nest (n = 3 observations) occurred when juveniles attained a mass of approximately 20 g. Feces contained insect remains. In the laboratory, individuals survived well on a diet of insects; they rejected fruits and seeds.

Liomys pictus.—The spiny pocket mouse, endemic to western Mexico (Hall, 1981), is the most common small mammal at the Chamela Biological Station. It was abundant in deciduous, thorn, and arroyo forests, and in crops, and present in other forest habitats. During the year, densities ranged from two to 71 individuals per ha in the deciduous forest, and from two to 61 individuals per ha in the arroyo forest. *L. pictus* is strictly terrestrial; no specimens were captured in traps set in trees. Nests (n = 30) were underground. The sex ratio did not differ significantly from 1:1 (N = 592, χ^2 = 0.6756, $d.f.$ = 1, $P > 0.05$). Males with scrotal testes and lactating or pregnant females were found throughout the year, but reproduction was concentrated during the dry season (Ceballos, 1989). Number of young in three litters was three, three, and five. Newborn young were pink, hairless, blind, and had a mass of approximately 2 g. During the first 38 days, total length and mass increased an average of 3.9 mm/day and 0.56 g/day, respectively (n = 5 young). In the laboratory, weaning occurred at 23 days of age.

The cheek pouches of approximately 200 individuals of *L. pictus* from the deciduous and arroyo forests contained 1,152 seeds, representing 26 families and 54 species of native plants. Seeds varied in size (greatest length) from 1 to 18 mm, and the number of seeds in the cheek pouches of an individual ranged from one to 87. The plant families most frequently represented were Leguminosae, Euphorbiaceae, and Convolvulaceae. The most abundant species were *Phaseolus microcarpus* (vine; 243 seeds = 21%), *Cyclantera multifoliolata* (vine; 237 seeds = 20.5%), *Ipomoea* sp. (vines; 353 seeds = 30.6%), and *Recchia mexicana* (tree; 42 seeds = 3.6%). Several of the species found in the pouches (e.g., *Caesalpinia eriostachys*) are known to contain toxic compounds and were rejected in feeding trials in the laboratory. Animals forced to eat these seeds decreased in mass and died in 3–5 days. On seven occasions small phoretic moths (*Psilopsaltis* sp.) were found on the dorsum of spiny pocket mice collected in the deciduous forest. One moth was on each mouse, except on two occasions, when two moths were on the same individual. Females of *P. santarosae* are phoretic on *L. salvini* in Costa Rica (Davis et al., 1986).

Nyctomys sumichrasti.—Vesper rats appear to be strictly arboreal. Only five individuals were caught, all in trees, at heights from 0.7 to 7 m above ground, and all in arroyo forest habitat. At the Chamela Biological Station, Collett et al. (1975) collected eight specimens in trees at heights from 1 to 3 m. Nests (n = 4) were similar to those of squirrels (*Sciurus*), constructed of leaves and plant fibers in the upper forks of trees. Reproduction in *N. sumichrasti* probably occurs throughout the year (Fleming, 1970; Genoways and Jones, 1972). Two females maintained in the laboratory each had a litter with two offspring. Young were pink, hairless, blind, and had a mass of approximately 4 g. During the first 5 weeks, offspring were attached continuously to their mothers' teats; this behavior is similar to that of other arboreal and semiarboreal small mammals, such as the Magdalena rat (*Xenomys nelsoni*) and probably represents a specialization for arboreality. Eyes opened at 18 days, weaning occurred at approximately 25 days, and adult body mass was attained after 8 weeks. In the wild, *N. sumichrasti* ate the hard fruits of the false evergreen needle bush

TABLE 1.—*Sampling effort (April 1986 to June 1987) and species composition of small-mammal fauna in different habitats in Chamela Biological Station, Jalisco, Mexico.*

	Habitat							
	Deciduous forest	Arroyo forest	Mangrove	Riparian forest	Palm forest	Thorn forest	Grassland	Annual and perennial crops
Total number of trapnights	10,080	10,080	720	720	720	720	576	720
Number of trapnights (traps on ground)	8,064	8,064	576	576	576	576	576	576
Number of trapnights (traps in trees)	2,016	2,016	144	144	144	144		144
Number of sampling periods	4	4	3	3	3	3	3	3
Number of species captured[a]	8	9	3	6	6	3	1	7

[a] Includes observations of *Sciurus colliaei*.

(*Jacquinia pungens*). Captive animals thrived and reproduced on a diet of oats, seeds, and fruits, including *Spondias purpurea, Cresentia alata,* and *Terminalia catappa*.

Oryzomys melanotis.—The black-eared rice rat was found in moist habitats. Density in mangrove and *Hippomane mancinella* forests during the dry season was 20 individuals per ha. Densities in arroyo forests ranged from 0 to 6.25 individuals per ha. The sex ratio did not differ significantly from 1:1 ($n = 12$, $\chi^2 = 3$, $d.f. = 1$, $P > 0.05$). Three individuals were seen to swim 2–10 m across channels, sometimes traveling as far as 100 cm underwater. *O. melanotis* is mainly terrestrial, but two individuals (8%) were caught in traps 70 cm above ground. Males with scrotal testes were collected from February to October, and a pregnant female was caught in March. The accepted diet in the laboratory consisted of seeds, leaves, and insects (Orthoptera).

Osgoodomys banderanus.—The Michoacan deer mouse is endemic to western Mexico and until recently was considered congeneric with *Peromyscus* (Carleton, 1980). It was common in the arroyo forest (densities ranged from 1.6 to eight individuals per ha) and scarce in the deciduous forest (less than one individual per ha); it was not captured in other habitats sampled. Its distribution was restricted to areas with rocks or large accumulations of brush on the ground. *O. banderanus* is semiarboreal, and most captures (95 = 66.5%) were in traps on the forest floor. Nests ($n = 6$) were spheroidal, lined with leaves and other plant material, and located in hollows of trees and under accumulations of litter on the forest floor. The sex ratio did not differ significantly from 1:1 ($n = 38$, $\chi^2 = 0.4705$, d.f. = 1, $P > 0.05$). Two pregnant females each had a single embryo. The accepted diet in the laboratory consisted of seeds, fruits, and insects (Orthoptera).

Peromyscus perfulvus.—The marsh deer mouse is endemic to Mexico (Hall, 1981). It was found mainly in wet habitats and is abundant in palm and arroyo forests; it was not captured in mangrove, thorn forest, or grassland habitats. Densities in arroyo forests fluctuated through the year from two to 14 individuals per ha. This species is semiarboreal; 85% (136) of the captures were in traps ≤5 m above ground. Nests ($n = 5$) were spherical, made with grasses and plant fibers, and were found in trees and in litter accumulations among vines. The sex ratio was strongly male biased (3.3:1, $n = 45$, $\chi^2 = 11.3076$, $d.f. = 1$, $P < 0.001$). Reproduction occurred throughout the year; pregnant females and males with scrotal testes were collected in all months. Litter sizes of three females maintained in the laboratory were two, three, and four young. Neonates ($n = 4$) weighed approximately 2–3 g, and were pink, hairless, and blind. Weaning occurred at approximately 25 days, and adult mass was attained after 7 weeks. Accepted diet in the laboratory included seeds, leaves, other plant material, and insects (Orthoptera).

Xenomys nelsoni.—The Magdalena rat is endemic to Mexico and is known from only three localities (Ceballos and Miranda, 1986; Hall, 1981). It is distributed patchily in the deciduous, arroyo, and thorn forests, occurring in areas with a high density of trees and woody vines, which it uses as arboreal runways. Nests ($n = 5$), found in hollows in trees (e.g., *Couepia polyandra, Caesalpinia eriostachys,* and *Cordia eleagnoides*), were spheroidal, made of grasses and fruit fibers (e.g., *Ceiba*). *X. nelsoni* is mostly arboreal; 22 captures (65%) were in trees, and the remainder in traps set on the ground; all captures on the ground were ≤40 cm from the base of a tree. *X. nelsoni* defecated and urinated in latrines, usually found in the forks of tree branches or in tree hollows.

Males with scrotal testes were caught in February, March, May, and September. A pregnant female was captured in August, and another in September. Females with offspring were captured in May and August and the mean litter size was 1.6 ($n = 5$ litters). Neonates were blind, hairless, pink, and had a mass of 5 g. The stomachs of two individuals contained finely ground green plant material.

Mammalian diversity in the Neotropics seems to be correlated with seasonality, productivity, and vertical and horizontal structure of the habitat (August, 1983; Ceballos, 1989). At Chamela Biological Station, the

habitats with the highest species richness were the arroyo and riparian forests; this pattern is similar to those found in other deciduous forest ecosystems (Bonoff and Janzen, 1980; Genoways and Jones, 1972). Deciduous and arroyo forests form a complex habitat mosaic rich in small mammals. The configuration of these habitats, and the specializations of the fauna and flora that reside therein, make the deciduous forest ecosystem unique among tropical biotas. Thus, preservation of deciduous forest habitats will contribute significantly to the conservation of biological diversity in the New World tropics.

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