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SMALL TERRESTRIAL RODENTS IN ELEVEN HABITATS IN SANTA ROSA NATIONAL PARK, COSTA RICA

by M. B. Bonoff and D. H. Janzen

Biology Department, Lewis and Clark College, Portland, Oregon 97219
Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104

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ABSTRACT

During the first 2 months of the rainy season, small terrestrial rodents *(Liomys salvini, Sigmodon hispidus, Oryzomys fulvescens)* were live-trapped in the 11 largest habitats in Santa Rosa National Park, Guanacaste Province, Costa Rica (Abandoned Horse Pasture, Upland Mixed Deciduous Forest, Unburned Grassland, Burned Grassland, Oak Forest Edge, Bosque Humido, Xeric Ridge, Lowland Mixed Deciduous Forest, Lowland Evergreen Forest, *Caesalpinia-Prosopis* Swamp, Mangrove Swamp). Small rodents occurred in all 11 habitats but at greatly differing densities. *L. salvini* was prominent in forest habitats and most abundant in Upland Mixed Deciduous Forest, but also occurred in non-forested habitats. *S. hispidus* was prominent in non-forested habitats, was most common in Abandoned Horse Pasture, and occurred sparsely in forested habitats. *O. palustris* occurred only in the habitats immediately adjacent to the ocean and was most abundant in Mangrove Swamp.

A seed or insect on the ground has very different chances of being encountered by a predaceous rodent in different habitats. Here we present the results of a rainy season live-trapping survey of species and quantity of small terrestrial rodents in 11 habitats in the largely deciduous forests and old pastures of Santa Rosa National Park (SRNP), Costa Rica. The study is part of a broad-spectrum attempt to understand the relationships between plants and the animals that eat them in the forests of this Park (e. g., Janzen 1980a, 1980b, Fleming and Heithaus 1978, Howe and Vande kerckhove 1979).

Methods and materials

Habitats

The 11 habitat types sampled encompass at least 90% of the habitat area of the Park. At a very general level, the Park is in deciduous forest with contained riparian

sites which range from evergreen to semi-deciduous. Additionally, the deciduous forest contains some tree and shrub species that are essentially evergreen (e. g., *Hymenaea courbaril, Andira inermis, Manilkara zapota, Ficus* spp., *Alibertia edulis, Jacquinia pungens).* Out of this forest were cut numerous pastures of 5-20 ha area several hundred years ago, leaving about two-thirds of the present Park area in forest. The cattle were removed from the Park in the 1977 rainy season, and now it is regenerating to forest except for the occasional fire that aids the persistance of the jaragua grasslands.

The eastern part of the Park lies on a plateau 300-350 m above sea level (referred to as "uplands" henceforth) and the western portion of the Park contains the steep slopes from this plateau to the small coastal plain and adjacent beaches ("lowland" habitats). Containing about 10,800 ha, the Park is a rough rectangle between the Pan-American highway and the Pacific Ocean and contains habitats generally representative of lowland Guanacaste Province.

Abandoned Horse Pasture. This site lies between the Park director's office and the park dining hall (comedor) in the SRPN administrative area. The patch of habitat is 100 x 50 m in area and is bordered on three sides by a one-lane paved road and on the fourth side by a heavily grazed horse pasture. The vegetation in this site was allowed to regenerate without further disturbance after the horses were removed in August of 1978. From at least 1972 to 1978 it was a heavily grazed but unburned horse pasture. The vegetation reached an average height of 1.5 m by January 1979 and was extremely dense. *Lantana camara* (Verbenaceae), *Melampodium divaricatum* (Compositae), and *Sida* spp. (Malvaceae) make up much of the bulk of the vegetation, with scattered individuals of *Mimosa pudica* (Mimosaceae), *Pisidium guineense* (Myrtaceae), *Cassia biflora* (Caesalpinaceae), *Acacia collinsii* (Mimosaceae), and numerous herbaceous plants (e. g., *Waltheria americana* (Sterculiaceae), *Turnera ulmifolia* (Turneraceae), *Passiflora pulchella* (Passifloraceae). Scattered through this dense thicket are 3-6 m tall trees of *Crescentia alata* (Bignoniaceae), *Acrocomia vinifera* (Palmae), *Guazuma ulmifolia* (Sterculiaceae), *Diphysa robinioides* (Fabaceae), and *Allophyllus occidentalis* (Sapindaceae). The east boundary is market by an old fencerow of *Gliricidium sepium* trees (Fabaceae). The vegetation is largely deciduous in the dry season, but even then very dense owing to the large number of small stems. Nearly all of the plants in this site produce seeds of potential food value to small mammals and there are numerous seedlings. Insects are also abundant and plant growth rates are among the highest for the Park during the rainy season.

Upland Mixed Deciduous Forest. This hilly habitat is crossed by several seasonal creeks and is clothed with secondary regeneration about 75 years old. It lies between the Monument and the main entrance road, and continues east to the Bosque Humido. The trapping site is along the easternmost portion of the Sendero Natural. The vegetation is dense and very irregular in height, being a mix of tree falls, heavily shaded sites below tall trees, and various ages of regeneration following small fires,

old roads and intense flooding. There is a thick litter of fallen leaves and branches, and scattered rock outcrops. The plants below 2 m height include *Acacia tenuifolia, A. collinsii, Machaerium biovulatum, Panicum maximum, Casearia corymbosa, C. sylvestris, Jatropha curcas, Aphelandra deppeana, Piper amalgo. Sapranthus palanga, Tetracera volubilis, Pychotria* spp., *Randia echinocarpa, R. karstenii, Rourea glabra, Selaginella* sp., *Banisteriopsis muricata, Forsteronia spicata, Serjania schiedeana* and *Byttneria catalpaefolia.* The tree overstory contains about 75 species (e. g., *Hymenaea courbaril, Andira inermis, Trichilia* spp., *Exostemma mexicana, Bursera simaruba, B. tomentosa, Luehea* spp., *Guazuma ulmifolia, Ateleia herbert-smithii, Calycophyllum candidissimum, Plumeria rubra, Hemiangium excelsum, Manilkara zapota, Chlorophora tinctoria, Bombacopsis quinata,* etc.). There is a heavy seed rain from all these plants and the insect density is very high as well.

Unburned Grassland. This site is 3 km southeast of the Park administration area, on the south side of the road to Playa Naranjo. It represents the hundreds of hectares of old cattle pasture that has been burned at 2-5 year intervals for the last century or more, but was not burned in the 1979 dry season. Cattle were removed from this habitat in 1977. The vegetation is almost entirely the introduced African grass, *Hyparrhenia rufa,* in a dense stand of last year's stems and new foliage 1-2 m in height. Scattered over the site at 10-50 m intervals are spreading *Crescentia alata* trees and in other similar sites *Byrsonima crassifolia, Ateleia herbert-smithii,* and *Curatella americana* are also scattered about in the vegetation. The site is bounded by small to very extensive patches of mixed deciduous forest. There are scattered open patches a few meters in diameter in the grassland, apparently caused by large rocks at or near the surface. Rodent food in this habitat is primarily grass blades, grass seed, small herb seed and insects. However, a few other seeds would be available from the trees and the adjacent wooded areas are close enough to forage in.

Burned Grassland. This habitat is identical to the unburned grassland except that it was burned in March 1979 (both were burned in March 1978). The vegetation is a dense sward of ungrazed 30 to 80 cm tall *Hyparrhenia rufa* with interspersed patches of dicot herbs (e. g., *Turnera ulmifolia, Sesbania emerus, Waltheria indica, Bidens riparia, Baltimora recta, Mimosa* spp.). Between the grass clumps the soil is hard, black, and generally free of litter. During heavy rain there may be as much as 1-3 cm of standing water on the ground surface. Seeds and fruits are scarce, with insects and leaves being the primary food available to a rodent at the time we trapped.

Oak Forest Edge. The eastern end of the Park was at one time clothed in a nearly pure stand of *Quercus oleoides* which was subsequently cleared to grass pasture mixed with small patches of oak forest. The trapping site is the grassland interface with one of these patches. It is about 4 km southwest of the east Park entrance. The grass is *Hyparrhenia rufa* mixed with other grasses and occasional shrubs. The trees are *Q. oleoides, Bursera tomentosa, Gliricidia sepium, Hemiangium excelsum, Ateleia herbert-smithii, Tabebuia ochracea, Lonchocarpus costaricensis, Cochlospermum vitifolium, Luehea* spp., etc. Below the canopy are many species of shrubs

(e. g., *Erythroylon, Acacia, Randia, Allophyllus, Alibertia, Calliandra).* There is abundant litter and the rocky soil probably provides abundant nest sites. Insects and seeds are abundant. Dry season fires occasionally remove the grass cover and burn into the forest at ground level.

Bosque Humido. Also called 'Bosque Siempre Verde', this heavily forested habitat lies on the generally south and west-facing slopes on the first break off the plateau about 5 km west of the main Park entrance. During the dry season this evergreen to semi-deciduous forest remains relatively cool and shady, and during the rainy season is the darkest and moistest habitat in the Park uplands, aside from creek beds. The forest canopy ranges from 10-25 m in height, and there is a dense understory of shrubs (e. g., *Calliandra emarginata, Sebastiana* aff. *confusa, Mouriri myrtilloides, Rourea glabra*). Most of the trees are evergreen except for a week or two when they change their leaves (e. g., *Hymenaea courbaril, Manilkara zapota, Castilla elastica, Sapium thelocarpum, Erblichia odorata, Brosimum alicastrum*). The soil is deep and well-drained, and covered with a thick litter and humus layer. Seeds, fruits and insects are probably as abundant in this habitat as in any forested habitat in the Park, and the rock piles, fallen logs and large pieces of litter provide cover and numerous nest sites. Where this forest is disturbed by tree falls, road cuts, landslides, etc., a dense and luxuriant tangle of second growth vegetation quickly takes over. Part of the trap line wound in and out of an edge between such a tangle and undisturbed forest.

Xeric Ridge. This habitat is approximately 15 km west of the administrative area of the Park and on the southern side of the 200 m ridge that lies between Playa Naranjo and Playa Nancite. It is reached by following the trail to Playa Nancite from its origin near the Playa Naranjo picnic area. The vegetation and terrain of this habitat are very different from that of the coastal flatland forest adjacent to it. The rocky soil is extremely well drained and more exposed to direct insolation than is the case in other habitats. This is the driest habitat in SRPN. *Bursera permollis,* a dry land derivative of the common tree species *Bursera simaruba* (Burseraceae), occurs only on this ridge. Other prominent plants are *Mimosa guanacastense* (Mimosaceae), *Bursera graveolens* (Burseraceae), *Melocactus maxonii* (Cactaceae), *Agave letonae* (Agavaceae), *Haematoxylon brasiletto* (Caesalpinaceae), and *Plumeria rubra* (Apocynaceae). In this habitat the trees and shrubs are 1-3 m in height. The transition from the ridge-side vegetation to the coastal alluvium is abrupt. High exposure to dry season winds, rapid rain runoff, and rocky substrate has produced a habitat with limited size, density, and number of plant species. Small mammal food is probably scarcer here than in any other non-burned habitat in the Park.

Lowland Deciduous Forest. This site is approximately 9 km west of the Park administration area and is reached by turning right for a kilometer after reaching the coastal alluvial plain on the road from the administration area to Playa Naranjo. While appearing to be mature forest in many areas, this lowland forest was grazed, selectively logged, and variously cleared in patches for fields during the past 100 years. The forest is almost entirely deciduous during the dry season and ranges from

5 to 35 m in height with a closed canopy. The understory is rich in shrub and small tree species (e. g., *Aphelandra deppeana, Casearia corymbosa, Allophyllus occidentalis, Psychotria* spp., *Randia* spp., *Piper* spp., *Acacia* spp., *Stemmadenia obovata, Acalypha garnieri, Hamelia patens*) and the saplings of overstory species. The canopy contains many large tree species (e.g., *Manilkara zapota, Thouinidium decandrum, Licania arborea, Enterolobium cyclocarpum, Andira inermis, Bursera simaruba, Bombacopsis quinata, Cocoloba* sp., *Guaicum sanctum, Tabebuia* spp., *Cedrela odorata, Swietenia macrophylla*). The forest floor is rich in fallen branches and smaller litter, and rodent nest sites are probably abundant. A rich seed fall and abundant insects should be available as food.

Lowland Evergreen Forest. This tall and very shady forest is 2 km south of the point at which the road to the beach arrives at the coastal lowlands. Only about 8 km² remain of this forest type, but it once covered much of the moister bottomlands. The general canopy, apparently undisturbed, is about 40 m tall and consists of *Pithecellobium saman, Brosimum alicastrum, Hura crepitans, Terminalia chiriquensis, Manilkara zapota,* and others. The understory shrub layer is rich in species of *Piper, Randia, Pisonia,* Euphorbiaceae, Apocynaceae, Sapindaceae, etc. Each of the overstory canopy trees is briefly leafless during the dry season, but leaflessness is not synchronized among species so the site remains relatively cool and shady throughout the year. There is much ground cover and there are fallen large pieces of litter, and insects and seeds are abundant.

Caesalpinia-Prosopis Swamp Forest. Approximately 3 km east of the north end of Playa Naranjo, this swamp forest lies immediately behind the mangrove swamps behind Playa Naranjo and its estuaries. The road to the north end of Playa Naranjo crosses the swamp forest immediately before it intersects briefly with the mangrove forest. The habitat is at least 40 ha in area and is clothed with a nearly pure stand of *Caesalpinia coriaria* and *Prosopis juliflora* 3-5 m in height. It is bordered on the inland side by species-rich deciduous and semi-evergreen forest. Scattered in the swamp forest are occasional individuals of *Lysiloma seemannii, Casearia corymbosa, Opuntia elatior* and *Pithecellobium saman.* There is essentially no ground cover except for fallen leaves and branches, and much of the ground surface is gray bare dry mud. Crab holes are very abundant, as are their occupants. During very high tides the site is occasionally briefly flooded with salt or brackish water; during very heavy rains as occur once or twice a year, the site is flooded with sheets of fresh water. Aside from crabs, and the fruits and seeds of *P. juliflora* and *C. coriaria* (falling in April-May), there is probably very little food in this habitat for a small rodent.

Mangrove Swamp. This habitat occupies the low areas behind Playa Naranjo that are occasionally (at least monthly) to frequently flooded by high tides. The vegetation is a nearly pure stand of black mangrove *(Avicennia nitida)* with scattered individuals of *Conocarpus erectus* and *Rhizophora mangle* (closer to the estuary). The ground is mud that is densely clothed in places with mangrove pneumatophores and heavily occupied by fiddler crabs. The trapping site is about 3 km southeast of the north end of Playa Naranjo, where the road crosses an extension of the mangrove

swamp. This habitat is immediately adjacent to the *Prosopis-Caesalpinia* swamp. The mangroves range from widely spaced with large areas of sun-baked mud in between, to a closed canopy that shades ever-wet mud. Insects and crabs are probably the only rodent foods available in quantity but the other habitats are within foraging distance. Owing to flooding at all times in the 24-hour cycle, mangrove swamp rodents probably use arboreal nest sites.

Season

The Park is subject to a severe dry season (late December through early May) during which almost no rain falls. The rainy season often contains a short dry spell in July but there was no evidence of this during the two months of trapping (21 May to 15 July 1979). The 1979 total precipitation will probably be higher than the usual 1800-2000 mm for the Park.

By trapping during the early rainy season, we were catching the most common small forest rodent, *Liomys salvini,* just after its annual breeding event (dry season and early wet season, January to mid-June, Fleming 1974), and therefore at the annual peak in density of foraging individuals. The most common grassland rodent, *Sigmodon hispidus,* breeds all year round and its annual cycle of density is unknown for SRNP. Additionally, we were trapping at the time of peak foliage and insect abundance, and minimum seed input.

Traplines

At 10 pace (about 5 m) intervals, 25 Sherman live traps (8 x 8 x 23 cm) were placed on the ground at the same marked 25 stations 3-5 times at 6-22 day intervals. They were always baited with dry oatmeal with fragments of peanut butter scattered through it. Traps were generally put out in the late afternoon and retrieved the next morning. The same kind of trap was used at all sites but the actual traps were replaced half way through the study when the original set was lost in a flooded river. Differences in trap availability to rodents within a single night were due to large cockroaches and dung beetles closing traps, and to the fact that a trap that has caught a member of one species is no longer available to catch a member of another species. Trapped animals were released at the point of capture except for three *Sigmodon hispidus* removed for laboratory experiments.

The original schedule was to be 6 nights of trapping at each of the 11 habitats, but mortar and machinegun fire prevented access to the lowland sites during the last half of the survey period.

Results

Four species of terrestrial small rodents were captured (Table 1): *Liomys salvini* (Heteromyidae), *Sigmodon hispidus, Oryzomys palustrus* and *Oryzomys fulvescens* (Cricetidae). *O. fulvescens,* a minute mouse, was captured only once (Abandoned Horse Pasture) and will not be considered further in this paper. The habitats also contain at least 4 other rodents (agouti, paca, variegated squirrel, and a climbing rat) but our survey did not include them.

Small rodents were caught in all 11 habitats, but the number trapped and species proportions varied greatly among habitats (Table 1). *O. palustris* was caught only in coastal habitats: Ridge, *Caesalpinia-prosopis* Swamp and Mangrove Swamp. It was caught at the highest frequency in the Mangrove Swamp (average 6.6% of the traps per night). On the Xeric Ridge *O. palustris* was one of two individuals trapped. At none of these sites was it ever caught at a frequency greater than 8% of the traps on a trap night.

Liomys salvini is clearly a forest mouse. *L. salvini* was consistently present in the forest traplines but was only occasionally caught in the grassland habitats and Abandoned Horse Pasture. Its highest frequency was in Mixed Upland Forest (27% of the traps caught *L. salvini* on an average night of trapping). *Sigmodon hispidus* is clearly a grassland rodent at SRNP. While frequently caught in low number in the forested habitats traplines, it was consistently caught in high numbers in the grassland and old pasture habitats. Its highest frequency was in the Abandoned Horse Pasture (51% of the traps caught *S. hispidus* on an average night of trapping).

Discussion

Liomys salvini is widely regarded as one of the most common small rodents in Central American lowland deciduous forests, and we found this to be the case in SRNP. However, we did not find it to be equally abundant in all forest types. It is tempting to suggest causes, but the great differences in *Liomys* abundance between quite similar appearing habitats (eg., Upland Mixed Deciduous and Lowland Mixed Deciduous, and between the Lowland Mixed Deciduous and Lowland Evergreen Forests) demands that a detailed study of food and cover needs to be made before such speculation is useful, except that the low density in the swamp habitats is probably due to flooding and nearly total lack of ground cover.

As Fleming (1970) and Goertz (1964) found in Panama and Oklahoma, *Sigmodon hispidus* was most abundant in non-forested habitats densely clothed in grass, dicot herbs and low shrubs. The occasional animal taken in forest may have been transient, or resident in a light gap (tree fall). Equally, the *L. salvini* taken in non-forested habitats may have been transients, or resident associated with isolated trees and small islands of large woody plants. *S. hispidus* was not trapped below

unbroken forest canopy and *L. salvini* was rarely or never taken in grassland hundreds of meters from forest edges and large woody plants.

As is reflected in its great climbing agility in a cage, *Oryzomys palustris* is much more of a climbing mouse than are *L. salvini* or *S. hispidus.* While this ability may be required for survival in the Mangrove Swamp habitat, it does not explain its restriction to the habitats close to the coast, one of which is the driest in the Park.

As a group, the 5 lowland habitats produced noticeably and significantly fewer rodents per trap nigh than did the upland habitats. This was especially striking in the contrast of Upland Mixed Deciduous with Lowland Mixed Deciduous forests. These sites are quite similar in plant species composition, physiognomy, microclimate, ground cover and light regime, yet the upland habitat produced about 5 times as many rodents per trap as did the lowland habitat.

Assuming that the numbers caught per trap are proportional to density, the Abandoned Horse Pasture and the Upland Mixed Deciduous Forest have the highest density of small terrestrial rodents of the 11 habitats, and the Xeric Ridge the lowest density.

In an on-going laboratory study, all three of these small rodents have been found to eat a wide variety of insects and seeds *(O. palustris* even eats live fiddler crabs*)*, but are quite careful about which species, sizes, etc. are eaten in which quantities (W. Hallwachs, personal communication). There is certainly no simple relationship such as *L. salvini* eats seeds and therefore lives in the forest and *S. hispidus* eats grass and therefore lives in the grassland.

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Resumen

Se presentan los resultados de un estudio comparativo de las densidades relativas entre las poblaciones de roedores pequeños en once hábitats del Parque Nacional de Santa Rosa, Provincia de Guanacaste, Costa Rica.

Durante los primeros dos meses de la estación lluviosa se capturaron vivos los roedores pequeños *Liomys salvini, Sigmodon hispidus, Oryzomys, palustris* y *O. fulvescens* de los siguientes sectores del Parque: Potrero del Caballo Abandonado, Bosque

mixto caducifolio de las partes altas, Potrero No Quemado, Potrero Quemado, Bosque de Encinos, Bosque Húmedo, Fila Muy Seca, Bosque Mixto Caducifolio de partes bajas, Bosque Verde de partes bajas, pantano de *Caesalpinia Prosopis* y, Manglar.

Aunque la mayoría de los roedores están representados en todos los sectores, las densidades relativas son muy diferentes. *Liomys salvini* es numeroso en las zonas boscosas pero más abundante en el bosque caducifolio mixto de las alturas. *S. hispidus* es el roedor preponderante en las zonas no boscosas, muy común en Caballo Abandonado y escaso en los bosques. *Oryzomys palustris* es más abundante en el manglar y zonas aledañas del litoral que en otros hábitats del Parque.

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Table 1. Percent of traps catching a species of rodent for each trapping night in 11 Santa Rosa National Park habitats (25 traps were used each night except nights 4 and 5 in the Abandoned House pasture when 23 were used, and night 4 in the Upland Mixed Deciduous Forest when 22 were used).

Upland sites

night	*L. salvini*	*S. hispidus*	night	*L. salvini*	*S. hispidus*
Abandoned Horse Pasture			**Unburned Grassland**		
1	12	52	1	0	20
2	4	60	2	0	24
3	8	52	3	0	44
4	4	39	4	0	8
5	9	52	5	0	20
$\bar{x}$	7	51	$\bar{x}$	0	23
S.D.	3.4	7.5	S.D.	0	13.0
Upland Mixed Deciduous Forest			**Burned grassland**		
1	24	4	1	16	8
2	32	8	2	0	16
3	36	4	3	8	32
4	13	9	4	8	24
5	32	4	5	8	24
$\bar{x}$	27	6	$\bar{x}$	8	21
S.D.	9.1	2.4	S.D.	5.6	9.1
Bosque Humido			**Oak Forest**		
1	32	0	1	40	12
2	6	8	2	20	8
3	4	4	3	16	8
4	28	0	4	8	12
5	20	8	5	12	4
$\bar{x}$	20	4	$\bar{x}$	19	9
S.D.	11.0	4.0	S.D.	12.4	3.3

Lowland Sites

Xeric Ridge

night	*L. salvini*	*S. hispidus*	*O. palustris*
1	0	0	0
2	0	0	0
3	0	0	0
4	4	0	4
$\bar{x}$	1	0	1
S.D.	2.0	0	2.0

Lowland Deciduous Forest

night	*L. salvini*	*S. hispidus*
1	4	0
2	4	0
3	4	8
$\bar{x}$	4	3
S.D.	0	4.6

Caesalpinia-Prosopis Swamp

1	4	0	0
2	0	0	4
3	0	4	4
4	4	0	4
$\bar{x}$	2	1	3
S.D.	2.3	2.0	2.0

Lowland Evergreen Forest

1	24	0
2	24	0
3	16	0
$\bar{x}$	21	0
S.D.	4.6	0

Mangrove Swamp

1	0	0	8
2	0	4	8
3	0	0	4
$\bar{x}$	0	1	7
S.D.	0	2.3	2.3