POPULATION ECOLOGY OF *PROECHIMYS GUAIRAE* (RODENTIA: ECHIMYIDAE)

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An ecological study of *Proechimys guairae* in Venezuela was made based on marking and recapturing of individuals at 225 trapping stations distributed over 9 ha. The trappability of individuals was >50% in most sampling events; there was no difference in capture rate between marked or unmarked individuals, or males and females. Adult individuals were present throughout the sampling period, but juveniles appeared at the beginning of the rainy season and disappeared in the dry season. Pregnant or lactating females were observed during most sampling periods. Most reproductive activity was concentrated from the middle of the dry season through the wet period. Estimated density was 1–3.5 individuals/ha; that variation appeared to be related to weather fluctuation and resource availability. Estimated effective population size (N_e) was 3–20 individuals/ha. Estimated home ranges value were significantly different for females and males. Adult females had no overlap of their home range, suggesting female territoriality. Home range of males did overlap. Data were compared with those of other species. Some ecological conditions that might have favored speciation guided by chromosomal mutations characterize *P. guairae*.

Key words: *Proechimys*, population ecology, home range, Venezuela

Proechimys is a common polytypic genus in the gallery forest of the Neotropical savannas. It is found <2,000 m above mean sea level from Nicaragua to Paraguay and Bolivia. The genus is one of the most numerous terrestrial mammals in a rainforest (Emmons, 1997). Some species frequently are used for food by local peoples. Some species also are important protozoan reservoirs, acting as etiological agents of serious and widely reported endemic rural illnesses (Leishmaniasis and Chagas disease) and in life cycle of forest viruses (Lainson and Shaw, 1974; Telford et al., 1975).

Studies of species of *Proechimys* in the wild have helped clarify aspects of their ecology: *P. semispinosus* from Panama (Adler, 1995, 1996; Adler and Beatty, 1997; Adler and Seamon, 1991; Adler et al., 1997; Fleming, 1970, 1971; Gliwicz, 1973, 1983, 1984; Tesh, 1970); *P. semispinosus* from Colombia (Alberico and González-M., 1993; González-M. and Alberico, 1993); *P. semispinosus* (= *guairae*—Aguilera et al.,

1995; Patton, 1987) from Venezuela (Eisenberg et al., 1979); *P. guyannensis trinitatis* (= *trinitatis*—Woods, 1993) from Trinidad (Everard and Tikasingh, 1973); *Proechimys* (2n = 62) from Venezuela (Díaz de Pascual, 1978); *P. brevicauda, P. hendeii*, and *P. longicaudatus* from Peru, Ecuador, and Brazil (Alho et al., 1986; Emmons, 1982); *P. guyannensis* and *P. cuvieri* from French Guiana (Charles-Dominique et al., 1981; Guillotin, 1982); *Proechimys* from Peru, Ecuador, and Brazil (Emmons, 1984); and *P. iheringi* from Brazil (Bergallo, 1995). Results of these studies indicate that these species, except for *P. semispinosus* from some islands of central Panama (Adler, 1996), have continuous annual reproduction. Population density, biomass, and home range were found to differ among species.

The existence in Venezuela of species of *Proechimys* that have experienced chromosomal speciation (Aguilera et al., 1995; Reig et al., 1980) points to an important

aspect of evolutionary theory related to ecological conditions required by speciation through chromosomal mutations. Begntsson and Bodmer (1976), Lande (1979, 1985), and Templeton (1980, 1981) considered that process possible only in populations that had low effective population size, high inbreeding, no gene flow, and low vagility. Results of ecological studies performed thus far do not reach any conclusion on these aspects. Thus, a study of basic structural and dynamic attributes of a population of *P. guairae* under natural conditions was carried out to gain insight into some of the ecological aspects affecting speciation.

MATERIALS AND METHODS

Study area.—The study area was located in Turiamo, Aragua, Venezuela (10°26′N; 67°50′ W), within the eastern limits of the Henry Pittier National Park. The climate was biseasonal, with a dry season between December and mid-April, followed by a wet season until November. The site, a semideciduous seasonal forest, was almost free of human intervention, had a flat topography, and was wide enough to ensure no insularity or habitat discontinuity.

Data collection.—Animals were sampled by marking and recapturing in a previously defined 9-ha grid of 225 sampling stations organized in 15 rows and 15 columns with 20-m between traps. A Tomahawk trap (48 by 16 by 16 cm) was placed at each sampling station. Sherman traps (28 by 8 by 8 cm) were placed at 135 of the sampling stations in nine consecutive rows to capture juveniles or small adults. Traps used per night totaled 360. Cassava and sometimes other fruits were used as bait. Traps were run for 7 consecutive nights each month for 20 months (50,400 trapnights).

Captured animals were identified by toe clipping. The following data were recorded for each individual: body weight; total length; length of tail; length of ear; length of left hind foot; pelage color and pattern; sex and sexual characteristics (size and position of testes of males; condition of vagina and mammae and pregnancy of females).

Data were used to: estimate the population's catchability (Jolly, 1965; Jolly and Dickson, 1983), maximum trappability (Krebs and Boon-

stra, 1984; Krebs et al., 1969), and minimum trappability (Hilborn et al., 1976); determine average percentage of captures and recaptures, number of captured individuals per month, maximum recapture frequencies and time between recapturing; determine the population's age and sexual structure; estimate population density by direct enumeration (Fleming, 1971; Krebs, 1966), population biomass through time and its effective size ($N_e = 4N_m N_f / (N_m + N_f)$, N_m = numbers of reproductive males and N_f = number of reproductive females—Thomas and Ballou, 1983); and estimate home ranges with minimum polygons (Stickel, 1954) and standard diameters (Hayne, 1949). Nonparametric analyses were used. The Kolmogorov-Smirnov two-sample test (*T*—Conover, 1980) was used to examine by sex catchability rates, rates of captures of captured (non-marked) and recaptured (marked) animals from the first to the last day of sampling of each session, maximum recapture frequency, and time between first and last recapture. Mann-Whitney *U* tests were used to compare total numbers and differences between sexes of marked and unmarked animals per month and home ranges. Result were considered significant at *P* < 0.05.

RESULTS

Five species of rodents were captured from May 1983 to December 1984 (Fig. 1) in the study area: *Proechimys guairae, Oryzomys talamancae, Oryzomys, Zygodontomys microtinus* (= *brevicauda*—Musser and Carleton, 1993), and *Heteromys anomalus*. During the study, 94 (48 males and 46 females) marked individuals of *P. guairae* were captured 275 times. Catchability (or trappability) of the *P. guairae* was estimated as the percentage of individuals known alive in a defined period and captured during that same period. Catchability was <50% on five occasions for males and three occasions for females. No statistical differences were found between catchability rates for males and females (*T* = 0.053, *P* > 0.05). Maximum trappability and minimum trappability were similar, 71.5% and 70.8%, respectively. Rates of captures of marked and unmarked animals were estimated from the accumulative average of marked and unmarked individuals captured
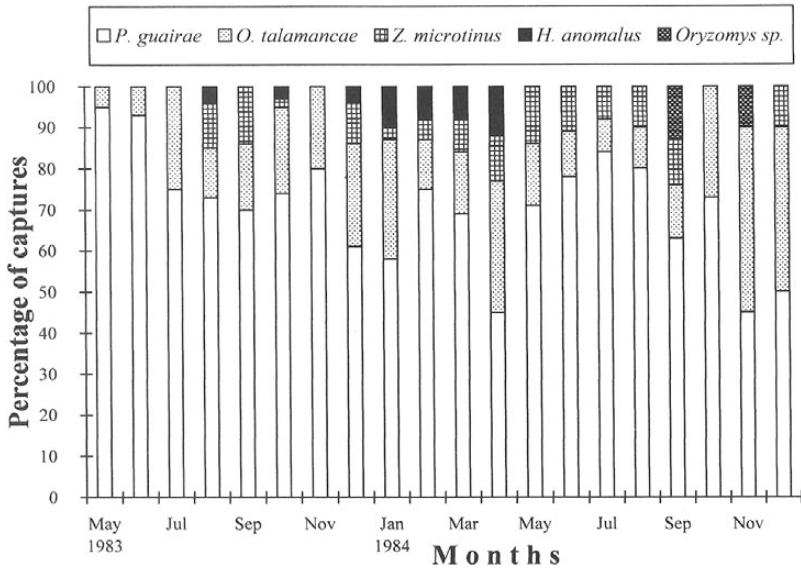
FIG. 1.—Species composition of the rodent community by month of capture in Turiamo, Aragua, Venezuela.

from the first until the last day of sampling of each session (Fleming, 1971); differences ($T = 0.9186$, $P < 0.05$) were found between marked and unmarked individuals. Results also showed that 50% of captures and recaptures was reached after the 3rd day of sampling.

Differences ($U = 88.0$, $P < 0.05$) were found among numbers of captured (unmarked) and recaptured (marked) *P. guairae* per month (Fig. 2), but no differences were found between males and females captured ($U = 124.0$, $P > 0.05$) and recaptured ($U = 199.0$, $P > 0.05$). Likewise,
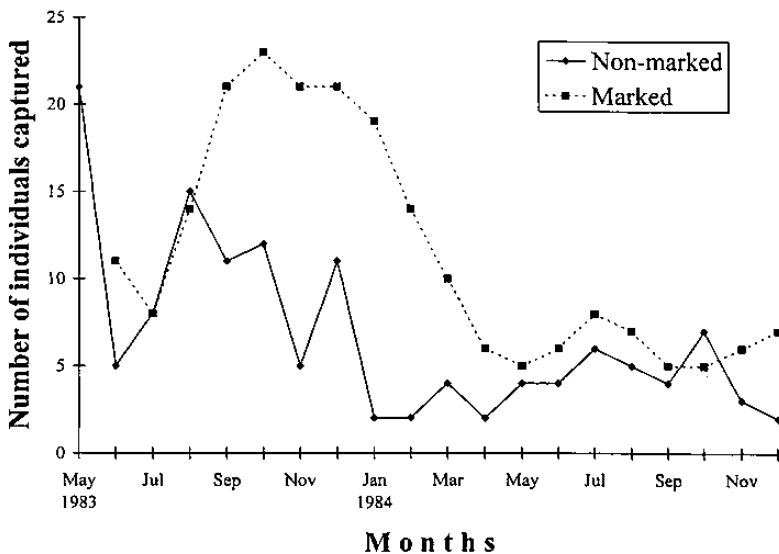
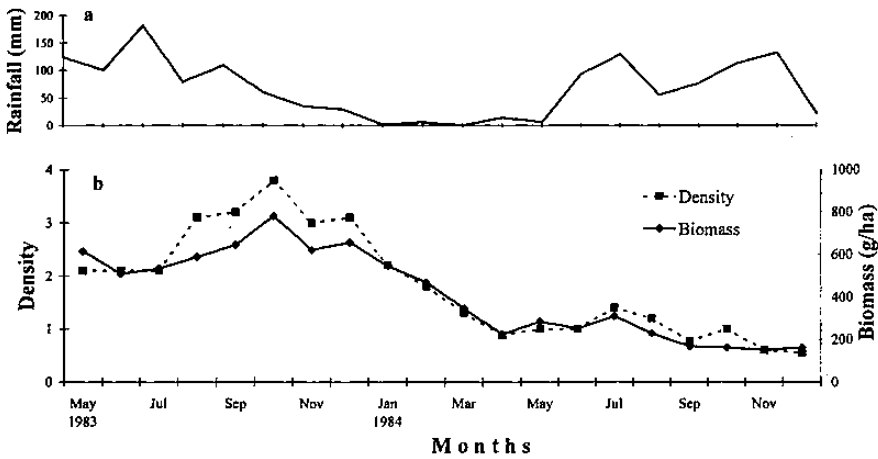FIG. 2.—Monthly numbers of *P. guairae* captured and recaptured each month in Turiamo, Aragua, Venezuela.

FIG. 3.—a) Mean monthly rainfall and b) estimated population density (individuals/ha) and biomass for *P. guairae* in Turiamo, Aragua, Venezuela.

there were no differences in the maximum frequency of recapture between sexes ($T = 0.375$, $P > 0.05$). The recapture period, the time that animals remained in the sampling area, was calculated as the time (in months) between first and last capture of a marked individual. It averaged 3–4 months. Time between first and last recapture was 1–4 months for 75% of the marked individuals, with 1-month interval most common. No differences were found ($T = 0.35$, $P > 0.05$) between males (range = 1–13 months) and females (range = 1–16 months).

The direct-enumeration method (Krebs, 1966) was used to compare our results with published data. That method was appropriate to obtain the minimum density value from the number of animals known in the

sampling area. The population of *P. guairae* increased during the 1983 wet season, reaching 3.6 individuals/ha, and decreased during the dry season (1 individual/ha; Fig. 3). That pattern was similar in 1984 but with lower absolute values, and density peaked near the beginning of the rainy season. Biomass, inferred by multiplying the average mass of all captured individuals by the estimated monthly density, was 150–750 g/ha.

Three age classes (Table 1) for each sex of *P. guairae* were established based on body mass, total length, reproductive condition, and pelage (Adler, 1994, 1996). Juveniles and subadults were found from the beginning of the wet season until the dry season (Fig. 4b) when only adults were trapped. Reproductive activity was main-

TABLE 1.—*Characteristics of sex and age classes of* Proechimys guairae.

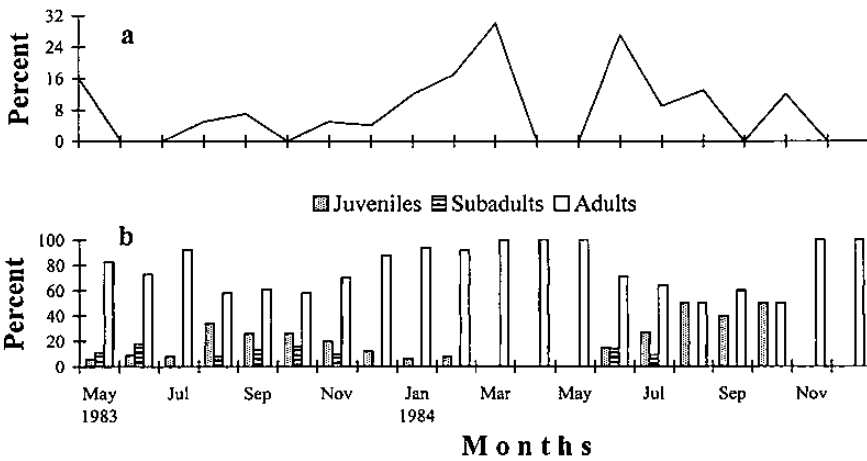|	Juveniles	Subadults	Adults
Males			
Body mass (g)	<120	121–200	>200
Total length (mm)	<160	161–200	>200
Reproductive condition (testes scrotal)	No	Yes-No	Yes
Females			
Body mass (g)	<130	131–200	>200
Total length (mm)	<160	161–200	>200
Reproductive condition (vagina open)	No	Yes-No	Yes

FIG. 4.—a) Percentages of pregnant and lactating females and b) age distribution by month for *P. guairae* in Turiamo, Aragua, Venezuela.

tained throughout the year (Fig. 4a), but activity decreased during the rainy season and peaked during the dry season.

The effective population size in the study area varied from 3 to 20 individuals/month. Home ranges of males (13 individuals) and females (11 individuals) were determined for animals captured five or more times. Home ranges of males (minimum area = 0.89 ± 0.20 ha; Fig. 5a) are larger than those of females (0.30 ± 0.05 ha, Fig. 5b; $U = 37.5$, $P < 0.05$). Males showed home-range overlap, which was not found in females, although some used the same home range in different periods during the year. Differences ($U = 30.0$, $P = 0.0167$) also were recorded for males (activity center = 2.26 ± 0.50 ha) and females (0.73 ± 0.25 ha) using Hayne's (1949) standard diameter, reinforcing the fact that females occupied smaller areas than males.

DISCUSSION

Composition of the rodent community is similar to that reported for other Neotropical ecosystems, shown as submontane forest (Díaz de Pascual, 1978) and deciduous forest in the Llanos region (Eisenberg et al.,
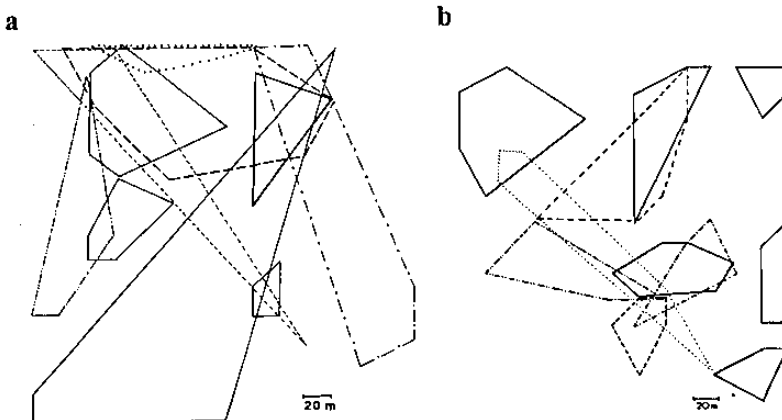

FIG. 5.—Minimal area polygons (reference) for a) male and b) female *P. guairae*; each polygons represents an individual.

1979). During the sampling period, the two most abundant species of the rodent community, *P. guairae* and *O. talamancae,* were present continuously (Fig. 1). Other authors (Adler, 1996; Adler and Seamon, 1991; Emmons, 1982; Fleming, 1971; Guillotin, 1982;) also have found *Proechimys* predominant in similar floristic and climatic environments.

Catchability of members of a population depends on multiple factors (Kikkawa, 1964). Trapping procedures, bait composition, and trap number and distribution were considered adequate relative to sampling times and frequencies; despite this, an evaluation of any kind of data bias is important. A quantitative estimation of catchability is necessary to assess if it is low (<50%) or high. Catchability of spiny rats in the present study remained >50% throughout the sampling period and thus can be considered high. These results contrast with low trappability found in *P. semispinosus* (Adler and Lambert, 1997). Average catchability can be considered relatively constant because maximum and minimum values are very similar (71%). High catchability also has been reported for other rodent species, such as *Microtus californicus* and *M. townsendii* (Krebs and Boonstra, 1984). My results showed that capture differences between non-marked and marked individuals were higher in the latter for both seasons (Fig. 2), indicating that toe clipping had no effect on trappability. Similar results also have been reported for other rodents (Korn, 1987). It is interesting that if 50% of captures and recaptures was reached in the 3rd day of sampling, sampling periods could be <1 week long, resulting in a lower average sampling effort. Neither numbers of monthly captured and recaptured individuals, nor maximum recapture frequencies, were significantly different between sexes. It can be concluded that male and female *P. guairae* have a similar response to trapping.

Forty-two percent of the marked population was recaptured only once (1 month in the sampling site), 12% was recaptured twice, and the rest of the population had a permanence period >3 months. Similar results were found for *P. semispinosus* (Fleming, 1971). Emmons (1982), using radio-tracking, found that some *Proechimys* are never recaptured despite months of continued presence after initial capture. As a general rule, males and females remained in the sampling area for an average of 3.5 months, but the most common was 1 month. Similar data (3.8 months) were obtained for *P. guyannensis* (Everard and Tikasingh, 1973). On the other hand, the average permanence time for *P. semispinosus* on several islands was 9 months (Adler et al., 1997). In Turiamo, at least one male stayed within the limits of the sampling area for 16 months; Adler (1996) reported one male *P. semispinosus* alive for 53 months. Permanence times for these species was estimated at ca. 1 year (Fleming, 1971), and this estimator can be used as a reference for minimal longevity rates (Fleming, 1971; Wolfe, 1985). The longer permanence time and longevity seen on the Gatun Lake islands (Panama) may be due to few predators and low competition (Adler, 1996). That situation was reversed in our study area, where many predators were observed.

Absence of statistical differences between capture and recapture rates of sexes suggests that the population maintained a 1:1 sex ratio during the sampling period. This differs from *P. semispinosus,* in which an excess of females on islands and an excess of males on the mainland is found (Adler, 1996). Characterization on the basis of mass, total length, and reproductive condition of different age classes for male and female of *P. guairae* showed no sexual dimorphism. This result is consistent with craniometrical analyses for the genus (Aguilera and Corti, 1995).

The age distribution of the population over time showed a clear pattern (Fig. 4). Adults are present year-around. Juveniles begin to appear during the rainy season (May–June) and become an important part of the population until the next dry season,

when it almost disappears. Subadults follow a similar pattern, only less defined in time. This population structure, in which juveniles are abundant during the wet season and almost absent during the dry period, has been found in other species, such as *Proechimys* (2n = 62) (Díaz de Pascual, 1978), *P. semispinosus* (Adler, 1994; Adler and Seamon, 1991; Fleming, 1971; Gliwicz, 1973), *P. guyannensis* (Guillotin, 1982), and *P. iheringi* (Bergallo, 1995). According to Fleming (1971), immature individuals have lower survival rates in the dry season; similar results (not reported here) were found for *P. guairae.* This may be due to a decrease in resource availability at this time of year, representing higher potential risk for juveniles than adults. During 1984, juveniles began to appear in our records during June. This apparent time displacement have might been due to that year's unusually long dry season (Fig. 3).

Reproductively active females were found throughout most of the 2-year sampling period (Fig. 4), but most were captured in May and June 1984, and one female with signs of pregnancy was captured three times in 1 year. Reproductive activity throughout the year has been reported for other *Proechimys* species under both laboratory (Weir, 1973) and natural (Table 2) conditions. Except for island populations of *P. semispinosus* (Adler, 1996; Adler and Beatty, 1997), breeding often did not occur all year and varied from 4 to 12 months; this reduction may have been a response to the very high densities on the islands. Results of my study, however, suggest that reproductive intensity is not stable during an annual cycle. It seems that reproductive activity is concentrated in the middle of the dry season and throughout the rainy season. This, together with a gestation of ca. 2 months (Weir, 1973), guarantees that juvenile emerge during the peak of resource availability. Similar results were reported for *P. semispinosus* in Panama (Adler and Seamon, 1991; Gliwicz, 1984).

The direct-enumeration method allows an estimate of the population's minimal number, considering only the sampled individuals. This method has been criticized and confronted with others such as the capture and recapture calendar (Jolly-Seber Model,—Seber, 1973). Hilborn et al. (1976) pointed out that the direct-enumeration method, under certain conditions, underestimated the population by 10–20%, if catchability was >50%. Even under unequal catchability rates, the Jolly-Seber Model is less biased than the total-enumeration method (Boonstra, 1985; Jolly and Dickson, 1983; Nichols and Pollock, 1983). In my study, the direct-enumeration method was followed because: it allowed direct comparisons with other reported data (Table 2); estimates based on the Jolly-Seber Model overestimated population size (15–100 individuals/ha); and, despite criticism, the direct-enumeration method remains a reliable estimator (Boonstra, 1985), especially when population numbers and recapturability are low (Krebs and Boonstra, 1984). In my study, population numbers were low, but a middle recapturability was found.

Estimated densities of *P. guairae* are very similar to those of *P. semispinosus, P. guyannensis, P. cuvieri, P. brevicauda, P. simonsi, P. iheringi,* and *P. longicaudatus* (Table 2). The reported densities of *P. semispinosus* from islands in Panama and *P. trinitatis* on Trinidad are quite high (7–58 individuals/ha). This might be due to the differences in resource abundance in those places that, according to Adler (1996), can influence density and mortality and consequently other population traits rather than differential evolution of life histories.

Climatic seasonality has been suggested as one of the most important factors influencing densities of rodent in forested habitats (Adler and Beatty, 1997; Everard and Tikasingh, 1973; Fleming, 1971; Guillotin, 1982). Ecological studies on Venezuelan rodents have shown that climatic variations, and consequently, habitat structural characteristics and resource abundance, have an influence on population parameters such as

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TABLE 2.—*Ecological studies of natural populations of species of* Proechimys. *MR: mark and recapture; O: observation; T: traps; C: census; M: male; F: female; NP: National Park.*

Species	Locality	Sampling	Duration (month)	Traps/night	Density (ind/ha)	Biomass (g/ha)	Home range (ha)	Reproduction	Source
P. semispinosus	Rodman and Sherman (Panamá)	MR	12	21,600	1.0–5.6	278–1,600	1.10 (M) 0.66 (F)	Year-round	Fleming, 1971
P. semispinosus	Isla Orquídea (Panamá)	MR	12	7,680	7.2–9.7	2,900		Year-round	Gliwcz, 1973, 1984
P. semispinosus	Islands in Gatun Lake (Panamá)	MR	12	22,447	12–58		0.145–0.217 (M) 0.075–0.2029 (F)	4–12 months/year	Adler, 1994, 1996; Adler et al. 1997 Adler and Beatty, 1997
P. semispinosus	Bajo Calima (Colombia)	MR	8	9,028	0.8–1.0		(0.29)	Year-round	Gonzalez and Alberico, 1993
P. semispinosus (= P. guairae)	NP Guatopo (Venezuela)	O-T	36		1.3–2.0	378–600			Eisenberg et al. 1979
P. guyannensis	Isla de Trinidad	MR	36	1,764	9.2–13.5		(0.17)	Year-round	Everard and Tikasingh, 1973
P. guyannensis and P. cuvieri	Saint Elie (Guyana Francesa)	MR	8		1.2–4.2	298–735		Year-round	Guillotin, 1982
P. iheringi	Iguape County (Brazil)	M-R	14	5,040	1.5–9.1	706	1.4 (M) 0.9 (F)	Year-round	Bergallo, 1994, 1995
P. brevicauda	NP Manu (Perú)	T-C	8		0.7–4.2		0.2–0.9 (M+F)		Emmons, 1982
P. hendeii					1.4–2.8	709	0.2–0.4 (M+F)		
P. longicaudatus									
P. longicaudatus	NP Brasilia (Brazil)	T	12	19,200			0.2 (M+F)		Albo et al., 1986
Proechimys sp. (2n = 62)	Barinitas (Venezuela)	T	15	708				Year-round	Díaz, 1978
P. guairae	Turiamo (Venezuela)	MR	20	50,400	1.0–3.6	150–750	0.9–2.3 (M) 0.3–0.7 (F)	Year-round	This study

density, age structure, and reproduction (Díaz de Pascual, 1978; Gómez, 1960; Soriano and Clulow, 1988; Vivas, 1986). Results of temporal fluctuations in population density in 1983 (Fig. 3) seem associated with climate and resource availability because high densities were observed during the rainy season and low densities in the dry season, while densities and rainfall in 1984 remained relatively constant. Another possible cause for low density is presence of predators such as large snakes (e.g., *Bothrops colombiensis, Pseudoboa neuwiidi*) and small cats (e.g., *Leopardus pardalis*). The maximum estimated biomass of *P. guairae* was similar to those found for *P. semispinosus, P. guyannensis, P. cuvieri, P. brevicauda, P. simonsi,* and *P. longicaudatus* (Table 2), but they were substantially lower than that reported for *P. semispinosus* in Panama (Fleming, 1971; Gliwicz, 1973, 1984).

Effective population size (N_e) is considered as the number of males and females born who survive and reproduce successfully in each generation (Reed et al., 1986). It has been suggested that a N_e of 50 is large enough to avoid excessive inbreeding, while a N_e of 500 is necessary to eliminate the effects of genetic drift (Frankel and Soule, 1981; Franklin, 1980). Effective sizes in my study might be underestimated by low capture rates (only 94 individuals in 20 months). Nevertheless, they can be considered as minimal values for a population of *P. guairae* (3–20 individuals/ha).

Home ranges for several members of the genus (*P. semispinosus, P. guyannensis, P. brevicauda, P. simonsi, P. iheringi,* and *P. longicaudatus*) have been estimated between 0.2–1.3 ha (Table 2). Home-range sizes of *P. guairae* differ between sexes (females, 0.3–0.7 ha; males, 0.9–2.3 ha). This difference in use of space between sexes also was reported for *P. brevicauda* and *P. iheringi* (Table 2). It allowed Gaulin and Fitzgerald (1986, 1989) to propose that natural selection could favor larger home ranges for males in populations with promis-

cuous or polygamous mating systems because competition among males for a suitable mate would be more intense. Another interesting result is that adult females do not have overlapping home ranges, while adult males do (Fig. 5). This behavior was reported by Fleming (1971) for *P. semispinosus,* Emmons (1982) for *P. brevicauda,* and Bergallo for *P. iheringi* (1995). This suggests territoriality and could be explained in terms of predictable and abundant feeding sources (Davies, 1978; Ostfeld, 1985), or in terms of maternal behavior (Wolff, 1993).

Spiny rats are a typical example of a genus with a high chromosomal diversity, and chromosomal changes have been invoked to explain its species richness. In the *P. guairae* complex, a linear pattern of chromosomal speciation was described (Aguilera et al., 1995; Reig et al., 1980). According to several authors (Bengtsson and Bodmer, 1976; Lande, 1979, 1985; Templeton 1980, 1981), the ecological conditions that might have favored speciation guided by chromosomal mutations are low N_e, low vagility, high inbreeding, and no gene flow. It is clear that population of *P. guairae* that I studied has a low N_e, and, according to data on home ranges and permanence in the study area, a low vagility. If this last feature is combined with the possible existence of a promiscuous mating system, it can be inferred that populations of *P. guairae* could maintain high inbreeding, and consequently, gene flow among populations could be low. Although it is possible to identify ecological characteristics that would help establish chromosomal speciation at present, it is not possible to assess if these were also present 50,000 years ago, when speciation of the superspecies *P. guairae* presumably occurred. Existence of molecular mechanisms of speciation (Rose and Doolittle, 1983) with less restrictive ecological conditions also supports the chromosomal speciation theory for this group.

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