DIFFERENCES IN HABITAT USE BETWEEN TWO MORPHOLOGICALLY SIMILAR TROPICAL FOREST RODENTS

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We examined differences in habitat use between two morphologically similar tropical forest rodents that have sympatric distributions. Mark-recapture techniques were used in Soberania National Park, Panama in a variety of forested habitats to characterize microhabitat use by Proechimys semispinosus (Central American spiny rat) and Hoplomys gymnurus (armored rat). P. semispinosus were distributed throughout the study area, but H. gymnurus were largely absent from ridgetops and the entire southern half of the study area. Canonical discriminant analysis showed that these two species used significantly different microhabitats. H. gymnurus were restricted to very wet, steep, and rocky microhabitats along streams within relatively undisturbed forest. P. semispinosus did not use microhabitats that were different from the overall available microhabitat and therefore exhibited a generalized pattern of microhabitat use. P. semispinosus rarely were captured along streams where H. gymnurus were most abundant. Differences in microhabitat use suggested that these two species may have physiological adaptations to preferred habitats.

Key words: Hoplomys gymnurus, Proechimys semispinosus, mating system, microhabitat, Panama, physiology

Versatility or degree of specialization in habitat use influences an organism’s ubiquity or distribution within its geographic range (MacNally, 1995). More versatile (more generalized) species generally maintain higher densities across a broader spectrum of habitats than do less versatile (more specialized) species. Individual- and population-level traits are often related to the degree of versatility in habitat use (Adler and Wilson, 1987; Seamon and Adler, 1996). Even closely related organisms often differ markedly in their habitat versatility. Determining the relationship between individual- and population-level traits and environmental structure (e.g., macrohabitat, microhabitat, and microclimates) is crucial to understanding differences in distributions of phylogenetically related species (Adler and Wilson, 1987; Lacher, 1981).

Ecological factors that determine distributions of tropical organisms and organization of tropical populations and communities are particularly complex (August, 1983; Leigh et al., 1993). Tropical rodents may serve as models for examining such variation in relation to environmental heterogeneity because they are often abundant and easily sampled and local diversity may sometimes be high. Proechimys semispinosus (Central American spiny rat) and Hoplomys gymnurus (armored rat) are morphologically similar frugivorous and granivorous rodents that have nearly coincident geographic ranges throughout much of Central America (Handley, 1966; Mendez, 1993). Within their respective ranges, these species are related more closely to each other than to any other species (Patton and Reig, 1989). These species coexist in several different forested habitats (Buchanan and Howell, 1965; Fleming, 1970; Gonzalez and Alberico, 1994). H. gymnurus have been reported to prefer wet undisturbed for-
ests, and *P. semispinosus* apparently are tolerant of a wider range of moisture and disturbance regimes and forest types (Adler, 1994; Alberico and Gonzalez, 1994; Buchanan and Howell, 1965; Fleming, 1970, 1971; Pine and Carter, 1970; Pitts, 1990). Thus, *P. semispinosus* are more versatile than *H. gymnurus*, despite their morphological similarities.

These two species are suited to examine distributions of tropical organisms in relation to environmental heterogeneity because one species is distributed widely and the other has a much more restricted distribution within their geographic ranges, and they are morphologically similar and often occur sympatrically. Our objective was to determine differences in microhabitat use between sympatric *H. gymnurus* and *P. semispinosus* that might explain why *P. semispinosus* are more ubiquitous than *H. gymnurus*.

**MATERIALS AND METHODS**

**Study area.**—This study was conducted along Pipeline Road in Soberania National Park, central Panama (9°10'N, 79°45'W, Fig. 1). Soberania National Park was a 22,000-ha tract of lowland tropical moist forest. Elevations ranged from ca. 30 m to 200 m (Karr, 1990). Pipeline Road was chosen because it provided convenient access to a variety of forest types and paralleled a southeast (relatively dry) to northwest (relatively wet) rainfall gradient. Although rainfall along that gradient was not measured during the study, long-term records at weather stations operated by the Panama Canal Commission paralleling the road in central Panama demonstrated such a gradient (Windsor, 1990). Mean annual rainfall at the weather station nearest the southern terminus of the road (the town of Gamboa, Fig. 1) was 2,188 mm, and mean annual rainfall at the weather station nearest the northern end of the study area (Salud Basin, Fig. 1) was 2,685 mm. Furthermore, changes in precipitation along the road were apparent based upon changes in species composition of trees. For instance, typically wet-habitat species (e.g., *Poulsea arnata*, *Welfia georgii*, and *Socratea exorrhiza [durissima]*) were a major component of the forest north of Río La Seda but were generally absent south of this stream.

Several small streams crossed the road throughout its length. The topography in the southern half of the study area was relatively flat, and the land gently sloped away from the streams. By contrast, the northern half (north of Río Limbo, Fig. 1) was composed of a series of hills, and streams occurred in steep ravines. The forest along the road was mostly second growth, but patches of old-growth forest remain along several streams and in other areas away from streams, particularly in the northern topographically diverse part of the study area. Thus, a gradient of more-disturbed forest (south of Río La Seda, Fig. 1) to less-disturbed secondary forest.

![Fig. 1.—Streams sampled that are within the study area on Pipeline Road. Inset shows the location of Soberania National Park and Pipeline Road in Panama (indicated by the arrow).](https://academic.oup.com/jmammal/article-abstract/79/3/953/859323/79085398323)
with patches of primary forest (north of Río La Seda, Fig. 1) followed Pipeline Road.

Climate of the study area was highly seasonal, with a pronounced dry season that generally occurred from the middle or end of December through April (Windsor, 1990). Over 90% of annual precipitation fell during the eight-month rainy season. Community-wide fruiting phenology within the forest coincided with seasonal rainfall (Foster, 1982), with very little fruit production at the end of the rainy season and beginning of the dry season. Fruit production was generally greatest at the end of the dry season and beginning of the rainy season.

Sampling methods.—Hoplomys gymnurus and P. semispinosus were sampled with live traps along a 17-km portion of Pipeline Road. For this purpose, 10 streams (Juan Grande, Frijolito, Frijoles, La Seda, Limbo, Mendoza, Sirystes, Macho, Pilón, and Agua Salud) crossing the road and their corresponding ridge tops were selected as sampling sites. Eighty ridge tops were sampled because those near Ríos Frijoles and La Seda were combined into one sample, and the ridge top adjacent to Río Pilón was not sampled. Eighteen transects were therefore sampled. Each transect was 800 m long with 20-m spacing of traps. Along each transect, 40 Tomahawk live-traps (40.5 by 12.6 by 13 cm) were set on the ground, and at every fourth station a second trap was set 1–2 m above the ground in a tree or liana. Arboreal traps were set to assess use of arboreal microhabitats by the two study species. Traps were baited with a piece of ripe banana mixed with peanut butter. During each sampling period, traps were set for four consecutive nights and checked each morning. Upon capture, animals were uniquely toe clipped, and sex, age (juvenile, subadult, or adult, as determined by pelage type, Adler, 1994), and reproductive condition (testes position for males, vaginal condition, symphysis condition, nipple size, and pregnancy for females) were recorded.

Sampling began in August 1994 and ended in January 1996. Sampling effort was distributed among sites such that each site was sampled during both wet and dry seasons. Thus, each site was sampled at least once in the wet season in 1994 and once in the dry season in 1995, except Río Pilón. That sampling site was added to the study in August 1995 and was sampled three times during the wet season in 1995. All other sites were sampled at least one more time in the wet season between August and December 1995, and Ríos Mendoza and Sirystes were sampled again at the beginning of the dry season in 1996. Variation in number of trapnights accumulated for each sampling period occurred due to various natural disturbances (especially flooding).

Structures of forest and microhabitat were characterized by measuring 18 microhabitat variables (Table 1) at each trap station along the 18 transects (Dueser and Shugart, 1978; Kelt et al., 1994). All variables were measured once during the study period.

Statistical analysis.—Relative abundances of H. gymnurus and P. semispinosus were calculated for each transect as numbers of individuals per 100 trapnights. Rock cover, log age, and gap variables were analyzed as dichotomous data. The tree-base classifications represented four different variables (round, stilt, buttress, and furrow) that could have a maximum of four counts in each of the classifications because four trees were sampled at each trap station (Table 1).

Stepwise-discriminant-function analysis (DFA) was used to select microhabitat variables that best described differential microhabitat use between the two species. That technique reduced the potential for confounding results with correlated variables in the subsequent analysis. Canonical discriminant analysis was then used to elucidate those differences in microhabitat use between species. Classes consisted of the two species and the overall available habitat. Captures of individuals at trap stations within a class represented samples of that class's microhabitat use. Only the first capture of each individual was used in the analysis.

Pairwise statistical differences among the three classes were determined by Mahalanobis multivariate distance measures and F-statistics (Kleinbaum et al., 1988). The relative contribution of variables from the stepwise DFA to the distribution of each class was determined by canonical discriminant analysis, and each significant canonical axis was analyzed for ecologically meaningful relationships among classes and microhabitat variables. Significance of individual variables responsible for separations among classes was determined by univariate analyses of variance (ANOVA), and overall significant differences in microhabitat use were determined by Wilks' Lambda F-statistics. We used t-tests to make univariate comparisons of...
### Table 1.—The 18 microhabitat variables used to characterize microhabitat use of *H. gymnurus* and *P. semispinosus* and the overall forest structure.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
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<tbody>
<tr>
<td>1. Gap</td>
<td>The presence or absence of an opening in the canopy caused by any disturbance</td>
</tr>
<tr>
<td>2. Microslope</td>
<td>The slope of the ground where the trap is placed, as measured by a clinometer</td>
</tr>
<tr>
<td>3. Rock cover</td>
<td>The presence of large rocks or boulders that cover &gt;25% of the area around the trap</td>
</tr>
<tr>
<td>4. Wood stems</td>
<td>The number of woody stems within 1 m² around the trap</td>
</tr>
<tr>
<td>5. Wood stems (1 m)</td>
<td>The same explanation as variable 4 except at 1 m above the ground</td>
</tr>
<tr>
<td>6. Herb stems</td>
<td>The same explanation as variable 4 except for herbaceous stems</td>
</tr>
<tr>
<td>7. Liana stems</td>
<td>The same explanation as variable 4 except for lianas and vines</td>
</tr>
<tr>
<td>8. Lianas (1 m)</td>
<td>The same explanation as variable 5 except for lianas and vines</td>
</tr>
<tr>
<td>9. Log distance</td>
<td>Distance in meters to the nearest log &gt;10 cm diameter</td>
</tr>
<tr>
<td>10. Log size</td>
<td>Size in centimeters of the nearest log &gt;10 cm diameter</td>
</tr>
<tr>
<td>11. Log age</td>
<td>An objective determination of fallen log age; recently fallen unrotting logs were classified as new: soft and rotting logs were classified as old</td>
</tr>
<tr>
<td>12. Tree distance</td>
<td>The distant in meters of the closest tree (&gt;10 cm dbh) to the trap in four directional quadrants around the trap</td>
</tr>
<tr>
<td>13. Tree size</td>
<td>The size in centimeters of the closest tree (&gt;10 cm dbh) to the trap in four directional quadrants around the trap</td>
</tr>
<tr>
<td>14. Tree base type</td>
<td>Four classifications of different shapes of tree bases: buttressed, stilt (roots are above the ground and form open spaces at the base of the tree), furrowed (deep folds in the boi of the tree and at the base of the tree), and rounded; each of the four trees measured in variables 12–13 were classified</td>
</tr>
<tr>
<td>15. Tree lianas</td>
<td>The number of liana stems at breast height on the trees measured for variables 12–13</td>
</tr>
<tr>
<td>16. Liana size</td>
<td>The diameter in centimeters of the largest liana supported by each of the four trees measured for variables 12–13</td>
</tr>
<tr>
<td>17. Canopy height</td>
<td>Height in meters of the canopy above the trap as determined by a distance rangefinder</td>
</tr>
<tr>
<td>18. Tree number</td>
<td>Number of trees (&gt;10 cm dbh) within 100 m² around the trap</td>
</tr>
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Habitat use with forest characteristics. Fisher’s exact test was used to analyze rocky habitat use by each species. All statistical procedures were conducted with SAS (SAS Institute, Inc., 1990).

**Results**

**Forest structure.**—Four forest-structure and microhabitat variables measured along streams exhibited gradients along Pipeline Road in our study area. Rock cover, stream bank slope, and canopy height increased from the drier southern end to the wetter northern end of Pipeline Road, but gap frequency along streams decreased along this same transect. Stream width was variable along Pipeline Road, ranging from a mean of 2 m on Río Macho to 10.6 m on Río Agua Salud.

**Distribution along Pipeline Road.**—A total of 9,664 trapnights of effort were performed along Pipeline Road over the duration of the study. We captured 46 *H. gymnurus* 50 times and 58 *P. semispinosus* 64 times. The only other rodents captured in this study were *Heteromys desmarestianus* (a forest spiny pocket mouse, captured five times). Only two *H. gymnurus* and no *P. semispinosus* were captured in arboreal traps. The two *H. gymnurus* were caught in traps on tree trunks (>25 cm dbh) that were at angles <45° relative to the ground and leaning over streams.

*Hoplomys gymnurus* were absent from streams south of Río La Seda and were most abundant at Ríos Mendoza, Sirystes, Macho, and Pilón (range = 0.95–2.0 individuals/100 trapnights, Fig. 2). Thus, *H. gymnurus* increased in abundance on stream transects northward along Pipeline Road except at Río Agua Salud, where their abundance declined sharply relative to the previous stream along the transect (Fig. 2). Only one *H. gymnurus* was captured at a ridge-top trap station (Sirystes), and that station was only 100 m from the stream.
Proechimys semispinosus were present both along streams and ridge tops but were most abundant along streams where \( H. \ gymnurus \) were absent (Juan Grande, Frijolito, and Frijoles) and ridge tops adjacent to streams where \( H. \ gymnurus \) were present (Mendoza, Sirystes, Macho, and Pilón, Fig. 2). The exception to this trend was at Río Agua Salud; \( P. \ semispinosus \) had their greatest abundance at Río Agua Salud both on the ridge top (2.6 individuals/100 trapnights) and along the stream (1.3 individuals/100 trapnights, Fig. 2).

Habitat use.—Hoplomys gymnurus and \( P. \ semispinosus \) used different microhabitats as determined by canonical discriminant analysis \( (F = 5.46, \text{ d.f.} = 8, 583, P < 0.0001) \), Fig. 3). Along the first canonical axis, \( H. \ gymnurus \) were associated with microhabitats with greater rock cover, steeper slopes, more stilt-based trees and ground vines, higher log density, and less round-based trees than \( P. \ semispinosus \) (Fig. 3). \( H. \ gymnurus \) used microhabitat that differed from the overall available habitat \( (F = 5.77, \text{ d.f.} = 8, 583, P < 0.0001) \), but \( P. \ semispinosus \) did not use microhabitat that differed from the overall available habitat \( (F = 1.73, \text{ d.f.} = 8, 583, P = 0.0874) \), Fig. 3).

To describe “optimal” microhabitat for \( H. \ gymnurus \), four different habitat classes were created based on relative abundance of \( H. \ gymnurus \) along each of the streams (Fig. 2). Stream habitats of \( H. \ gymnurus \) (Fig. 4) included Ríos Mendoza, Sirystes, Macho, and Pilón (greatest abundances of \( H. \ gymnurus \)). Río Agua Salud and marginal-habitat streams (Ríos Limbo/Hunt Club and Río La Seda, Fig. 4) were streams where \( H. \ gymnurus \) were captured infrequently relative to stream habitats of \( H. \ gymnurus \). Stream habitats of \( P. \ semispinosus \) (Fig. 4) were where \( H. \ gymnurus \) were never caught and included Ríos Juan Grande, Frijolito, and Frijoles.

Microhabitat use by \( H. \ gymnurus \) differed from all habitat types (\( P. \ semispino-
Fig. 3.—Canonical discriminant analysis of microhabitat use by *H. gymnurus* and *P. semispinosus*. The proportion of the analysis each canonical variate explains is in parentheses along each axis. Significant axes are denoted by asterisks (*P < 0.05, **P < 0.01, ***P < 0.001, ****P < 0.0001). Variables that significantly contribute to species separation are listed along axes in which they are most highly correlated. All variables displayed are at least significant at *P < 0.05*. Each axis represents a gradient of habitat characteristics that correlates with each species’ habitat use (overall habitat segregation as determined by Wilks’ Lambda multivariate approximation: *F* = 3.85, *d.f.* = 16, 1166, *P* < 0.0001). Classes of forest structure are denoted by empty squares, and animal classes are denoted by filled circles. Standard error bars are presented for each class.

*P. semispinosus* streams—*F* = 6.65, *d.f.* = 17, 348, *P* < 0.0001; Agua Salud—*F* = 2.53, *d.f.* = 17, 348, *P* = 0.0008; marginal habitat streams—*F* = 4.25, *d.f.* = 17, 348, *P* < 0.0001) except *H. gymnurus* stream habitat (*F* = 1.28, *d.f.* = 17, 348, *P* = 0.20). Stream habitat of *H. gymnurus* differed from stream habitat of *P. semispinosus* (*F* = 9.89, *d.f.* = 17, 348, *P* < 0.0001, Fig. 4). Along the first canonical axis, stream habitat of *H. gymnurus* was characterized by greater rock cover, trees with buttress and stilt bases, more logs, and higher canopy height, while stream habitat of *P. semispinosus* was characterized by greater density and size of lianas, fewer logs, and more trees with round bases (Fig. 4). Marginal stream habitats of *H. gymnurus* were intermediate along that gradient and separated along the second canonical axis, with Rio Agua Salud having larger trees, more herbaceous growth and logs, and higher densities of trees and stems at 1 m than the marginal-habitat streams (*F* = 4.52, *d.f.* = 17, 348, *P* < 0.0001, Fig. 4).

*Hoplooms gymnurus* were associated with rock cover, canopy height, and slope. Those three variables had higher values in stream habitats with relatively high abundances of *H. gymnurus* (Fig. 4) than in stream habitats of *P. semispinosus* (univariate *t*-tests—slope: *X* = 17.02° ± 1.12 SE, *n* = 127 versus *X* = 11.1° ± 1.02 SE, *n* = 94, *t* = 3.96, *P* = 0.002; canopy height: *X* = 21.7 m ± 0.68 SE, *n* = 127 versus *X* = 17.0 ± 0.71 SE, *n* = 94, *t* = 4.82, *P* <
0.0001; Fisher's exact tests—proportion of trap stations with 25% rock cover 32.3%, n = 127 versus 3.5%, n = 94, $\chi^2 = 9.08$, d.f. = 1, $P < 0.0001$. Hoplomys gymnurus occurred at trap stations with higher proportions of rock cover than available in stream habitats of H. gymnurus (50.0%, n = 46 versus 32.3%, n = 127, $\chi^2 = 4.99$, d.f. = 1, $P = 0.032$). Canopy-height and slope variables did not differ in that comparison ($P > 0.05$). In stream habitats, H. gymnurus (50.0%, n = 46) occurred at trap stations with rock cover at a greater frequency than P. semispinosus (19.1%, $\chi^2 = 4.76$, d.f. = 1, $P = 0.04$, n = 16). Canopy-height and slope variables did not differ in that comparison ($P > 0.05$).

**DISCUSSION**

Although samples in our study were small because of low abundances of both species, we found distinct differences in habitat associations between H. gymnurus and P. semispinosus. These two species used significantly different microhabitats (Fig. 3) and had different optimal habitats (H. gymnurus were more restricted in microdistribution, Fig. 4). H. gymnurus were restricted to streams on the wetter and less disturbed northern section of the study area on Pipeline Road. Along streams where H. gymnurus were present, P. semispinosus were rarely caught except at Río Agua Salud. Proechimys semispinosus were numerically dominant along disturbed streams and ridge tops. Rarity of P. semispinosus along H. gymnurus streams could be the result of interspecific competition or adaptations to different habitats.

It has been assumed that competition for food resources among frugivorous mammals plays a large role in organization of mammalian communities in the tropics (Smythe, 1986), and the superficial similarities (i.e., diet, morphology, and largely overlapping geographical distribution) between H. gymnurus and P. semispinosus suggest that these two species may be competitors. However, abundances of both species in this study were very low relative to other studies of P. semispinosus (e.g., average density of eight island populations of P. semispinosus near the study area peaked at 29 individuals/ha—Adler, 1996; Gliwicz, 1984). By contrast, Fleming's (1970) study of mainland rodent communities in central Panama yielded comparably low abundances (H. gymnurus were rare and not caught on his main study grid; P. semispinosus densities ranged from 0.44 to 5.6/ha). Intense competition between these species in the study area seems unlikely due to the low abundances reported during the study period.

This study suggests that H. gymnurus and P. semispinosus are adapted to different microenvironments. P. semispinosus have been reported to be generalists that occur in many different forested habitats (Adler, 1994; Fleming, 1971). This pattern was supported in our study, but P. semispinosus may be better adapted to drier habitats because they were much less abundant in the wetter stream sites numerically dominated by H. gymnurus.

Several specific habitat requirements for H. gymnurus were revealed in this study. This species was restricted to streams, primarily those with steep slopes, a tall canopy covering the entire stream, relatively few gaps, and extensive rock cover. Furthermore, H. gymnurus were captured at trap stations with rock cover at a greater frequency than was available along those streams. H. gymnurus had been reported previously to associate with primary forest (Alberico and Gonzalez, 1994), and the association with steep rocky slopes along streams was consistent with Emmons' (1990) observation that H. gymnurus appear to prefer wet locations, rocks, and stream sides. This pattern prevailed even in pristine old-growth seasonally dry forest in Darién, eastern Panamá, where we captured this species only along rocky streams. We also have captured H. gymnurus away from streams in large tracts of young forest on the perennially wet Pacific slope of Colom-
bia and in very wet primary forest in central Panama. It is possible that the stream microhabitat and tall canopy in less disturbed drier forests creates a "valley effect," providing a cool, damp environment that is preferred by this species. Although no comparative physiological studies have been conducted within the echimyid family, *H. gymnurus* may be adapted physiologically to relatively cool and wet environments and are intolerant of drier sites. The rocky habitat also may provide a specific requirement for reproduction, such as adequate protection for nesting and young.

In conclusion, *H. gymnurus* appear to be restricted to very wet rocky microhabitats in both secondary and primary forest. Differences between *H. gymnurus* and *P. semi­spinosus* suggest that both species have physiological adaptations to their respective preferred habitats.

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**LITERATURE CITED**


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