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SHORT COMMUNICATION

Ecology of two species of echimyid rodents (*Hoplomys gymnurus* and *Proechimys semispinosus*) in central Panamá

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The family Echimyidae is one of the most widely distributed rodent families in the Neotropics. Virtually every tropical lowland forest contains at least one echimyid species, and many areas contain half a dozen or more species. The commonest terrestrial representatives of the family are within the genus *Proechimys*, and several species such as *Proechimys semispinosus* (Central American spiny rat) have been the subject of intensive ecological studies (e.g. Adler 1994, 1996; Adler & Beatty 1997, Alberico & Gonzalez 1993, Fleming 1971, Gliwicz 1984, Gonzalez-M. & Alberico 1993). *P. semispinosus* is often the most abundant rodent throughout its geographic range in Central America and northwestern South America, and its ecology is now fairly well-known.

The geographic range of *P. semispinosus* is nearly coincident with that of another terrestrial echimyid (Handley 1966), *Hoplomys gymnurus* (the armoured rat), whose ecology is largely unknown. These two species are morphologically quite similar, the major external difference being the presence of much larger spines on the dorsum of *H. gymnurus*. They are also phylogenetically more closely related to each other than to any other rodents within their ranges (Patton & Reig 1989) and may not be distinct at the generic level (Gardner & Emmons 1984). Despite the morphological similarities, *H. gymnurus* apparently has a much more restricted distribution within the geographic range and is found only in very moist situations (Buchanan & Howell 1965, Emmons 1990, Pine & Carter 1970, Tomblin & Adler 1998). In regions that experience a pronounced dry season, this species is restricted to cool, moist ravines (Tomblin & Adler 1998), while *P. semispinosus* is found within virtually any forested habitat (Adler 1996, Adler & Seamon 1991, Fleming 1971). In this report, we compare sex ratios, body weights, tail loss and spatial distributions of these two echimyids where they occur sympatrically within a lowland tropical forest in central Panamá.

This study was conducted in the Pipeline Road region within Soberania National Park, a 22,000-ha tract of tropical moist forest in central Panamá at 9°10′N, 79°45′W. Pipeline Road runs from southeast to northwest and provides access to a mosaic of second-growth forest of varying ages and patches of old-growth forest. Elevation along the road ranges from *c.* 30–200 m (Karr 1990), and annual rainfall ranges from a mean of 2188 mm at the southern terminus of the road (the town of Gamboa) to 2685 mm at the northern end of our study area (Río Agua Salud) (Windsor 1990). The area is highly seasonal with respect to precipitation and experiences a pronounced 4-mo dry season during which < 10% of annual precipitation occurs.

Topography changes from the flat southern half to the hilly northern half of the study area. A series of 11 streams crosses the section of Pipeline Road within our study area. In the hilly region, the streams lie within steep ravines that provide a cooler and moister microclimate, to which *H. gymnurus* is restricted (Tomblin & Adler 1998).

We sampled *H. gymnurus* and *P. semispinosus* populations by live-trapping along transects during three distinct periods. During each period, a single Tomahawk live-trap (38.4 cm × 12.0 cm × 12.0 cm) baited with cut ripe banana or plantain and peanut butter was set on the ground at each trap station, with an intertrap distance of 20 m. The first period was a preliminary sampling during the dry season in December 1990 and January–February 1991 along two streams (Río Limbo/Hunt Club and Río Agua Salud) in the northern half of the study area and two sites away from streams in the southern half of the area. Transects were 25 stations in length, and each site was sampled only once for one to three consecutive nights during this preliminary effort. The second period was a more intensive sampling effort that provided the majority of the data set. This period ran from August 1994 to January 1996 in which 18 sites along 10 streams (Quebrada Juan Grande and Ríos Frijolito, Frijoles, La Seda, Limbo/Hunt Club, Mendoza, Sirystes, Macho, Pilón and Agua Salud) were sampled. A single transect of 40 stations ran along each stream, and another 40-station transect ran along a ridgetop adjacent to each stream (except the Río Pilón, which was sampled using a single streamside transect). A single ridgetop between Ríos Frijoles and La Seda was sampled because of the close proximity of these two streams to each other. Each of these 18 transects was sampled for four consecutive nights at least three times during both the rainy and dry seasons. The third period was a short but intensive effort in the rainy season in June and July 1997 to increase the sample of *H. gymnurus*, whereby sampling was conducted along two streams where *H. gymnurus* was most abundant during the second sampling period. Transects were 75 stations in length, and traps were set for 10 consecutive nights.

All captured *P. semispinosus* and *H. gymnurus* were uniquely toe-clipped for permanent identification; sex, body mass, age class, reproductive condition and tail status were determined before they were released at their station of capture. Age class (juvenile, subadult or adult) was determined on the basis of pelage (e.g. Adler 1994, Tomblin & Adler 1998). Reproductive data included testes position in males and vaginal patency, enlarged lactation tissue, and obvious pregnancy in females. Tail status was recorded as presence or absence since tail autotomy occurs in both species.

We first examined sex ratios of the two species using chi-squared analysis and included each individual only once in this analysis. We then examined body weights of the two species. In this analysis, we included only the greatest body weight reached by an individual during the study. Thus, an individual was included in this analysis only once, which avoided repeated measures. Body weights of adult males and females (including pregnant females) were compared between and within the two species using two-way analysis of variance. Body-weight distributions of young (juveniles and subadults were combined as young because of the small numbers of captures) and adults of both sexes were also examined to determine minimum and maximum weights for young and adults. Frequencies of tailed and tailless individuals were compared between species using chi-squared analysis. Each individual was included in this analysis only once; if an individual captured more than once lost its tail between subsequent captures, it was included in the analysis as a tailless individual. We lumped sexes and age classes for this analysis because of the small sample sizes.

We analyzed spatial distributions of both species using nearest-neighbour distances of individuals within a species along the transects sampled during the second sampling period. Thus, animals caught in adjacent traps would have a nearest-neighbour distance of 20 m, and animals caught at the same trap station would have a distance of 0 m. A relatively low mean nearest-neighbour distance within a species indicated a closer spatial association of individuals of that species. Wilcoxon's rank sum test was used to analyze these data because distributions were not normal. We conducted three separate analyses in which we included (1) all individuals of the two species, (2) all individuals excluding young because young could potentially represent dispersal patterns that would skew results, and (3) distances of adult males to the nearest adult females.

We captured 64 *H. gymnurus* 67 times and 83 *P. semispinosus* 88 times in over 11,000 trapnights. *H. gymnurus* was captured only in the northern half of the study area, and all but one individual were captured along stream transects. *P. semispinosus* was captured throughout the study area, but only one individual was captured along the Río Pilón, and none were captured within the streamside transects along the Ríos Mendoza and Sirystes. *P. semispinosus* was more abundant over the entire study area, but *H. gymnurus* was locally more abundant than *P. semispinosus* along the Ríos Limbo/Hunt Club, Mendoza, Sirystes, Macho, and Pilón (Tomblin & Adler 1998). Greatest relative abundances per transect during the second sampling period were 2.6 *P. semispinosus* per 100 trapnights along the Agua Salud and 2.0 *H. gymnurus* along the Río Pilon.

The sex ratio did not differ from 1 : 1 in either species (51.7% of *H. gymnurus* and 51.2% of *P. semispinosus* were male; $\chi^2 = 0.001$, df = 1, P = 0.995). Adult body weights differed between the two species (F = 30.77, df = 1, P < 0.0001). The largest male *P. semispinosus* reached 620 g, while the largest male *H. gymnurus* attained the enormous size of 815 g in July 1997. This *H. gymnurus* was first captured as a 353-g adult in February 1995. Adult males of both species were larger than adult females, even when pregnant females were included (F = 31.02, df = 1, P < 0.0001). The interaction was significant (F = 5.87, df = 1, P = 0.0170) because male *P. semispinosus* were larger on average than female *H. gymnurus*. There was very little overlap in body weights of young and adults (as

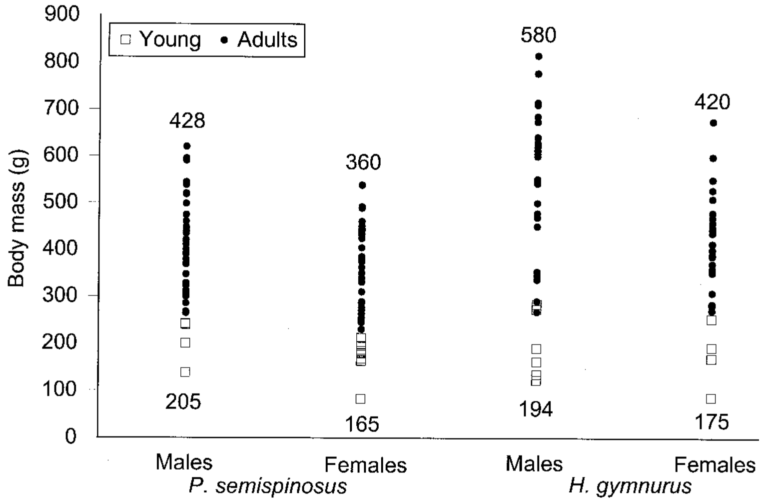

Figure 1. Body-weight distributions of all individual *H. gymnurus* and *P. semispinosus* captured in the Pipeline Road study area in central Panamá. Age classes (young includes juveniles and subadults) were based on pelage characteristics. Numbers above and below the data points represent mean body weights of adults and young, respectively.

determined by pelage characteristics) of either species (Figure 1). Only *H. gymnurus* young and adult males overlapped in body weight. Tailless individuals comprised 9.4% of the *H. gymnurus* sample and 17.9% of the *P. semispinosus* sample. This difference was not statistically significant ($\chi^2 = 2.146$, df = 1, P = 0.143).

The nearest-neighbour distances with all individuals included did not differ between the two species (*H. gymnurus*: mean = 35.5 m, SE = 8.2, n = 40; *P. semispinosus*: mean = 54.8 m, SE = 11.1, n = 54; z = −1.29, P = 0.197). With young removed from the analysis, distances again did not differ between the two species (*H. gymnurus*: mean = 32.9 m, SE = 8.8, n = 34; *P. semispinosus*: mean =

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56.5 m, SE = 11.8, n = 46; z = −1.49, P = 0.137). However, adult male *H. gymnurus* distances to the nearest adult female (mean = 50.6 m, SE = 16.2, n = 17) differed from those of *P. semispinosus* (mean = 124.8 m, SE = 22.8, n = 25; z = −2.17, P = 0.03). Thus, *H. gymnurus* males and females were more closely associated with each other than were the sexes of *P. semispinosus*.

H. gymnurus was generally less abundant and more restricted in its distribution than was *P. semispinosus*. The most important ecological difference between these two species in this seasonally dry forest appeared to be the requirement of *H. gymnurus* for cool moist microhabitats beside streams in steep ravines. Within these moist situations, *H. gymnurus* was associated with rocky microhabitats and more mature and taller forest, while *P. semispinosus* used microhabitat that was not different from available microhabitat within the study area (Tomblin & Adler 1998). The restricted distribution of *H. gymnurus* within this seasonally dry forest demonstrated that this echimyid was more specialized than *P. semispinosus* with respect to habitat use and suggested that this species may have been physiologically constrained to such moist habitats (Tomblin & Adler 1998). A more concentrated effort in appropriate habitat was therefore necessary to acquire a large sample of *H. gymnurus*.

We accumulated other ecological information that had not been previously reported from sympatric populations of these two species. Nowak (1991) reported a body weight of 450 g for *H. gymnurus*, and Emmons (1990) reported a maximum weight of 790 g for this species. The maximum weight of 815 g in our study apparently represented the largest size yet reported for *H. gymnurus*. The maximum male body weight of 620 g for *P. semispinosus* in our study was larger than that of 550 g reported by Emmons (1990) for any *Proechimys* species but was smaller than the maximum of 720 g reported by Adler (1996) from populations on small islands in central Panamá. Adult male *H. gymnurus* were approximately 36% larger on average than adult male *P. semispinosus*. Adult males of both species were larger than females, even when pregnant individuals were included, a finding consistent with both Emmons (1990) and Nowak (1991). Adult male *H. gymnurus* were on average 38% larger than females, and adult male *P. semispinosus* were 19% larger than females. Because there was very little overlap in body weight between young and adults, weight served as an indirect indicator of age class for both species. Thus, in these populations the threshold body weight between young and adult *H. gymnurus* was *c.* 270 and 260 g for males and females, respectively. For *P. semispinosus*, threshold body weights were *c.* 250 and 220 g for males and females, respectively.

The rate of tail loss in the *P. semispinosus* population (17.9%) was similar to previously-reported rates for this species in central Panamá. For instance, Fleming (1971) found that 18% of all individuals were tailless at two mainland sites, and Adler & Seamon (1991) found that 16% of individuals on small islands were tailless. Rates of tail loss have not been previously reported for

H. gymnurus. Although the rate of tail loss was only slightly more than half that of *P. semispinosus*, the difference was not statistically significant. However, sample sizes were small, and based on sampling in other locations in Panamá, it appeared as though *P. semispinosus* did indeeed lose their tails more frequently than did *H. gymnurus*. Predation and intraspecific aggression have been invoked as the most likely causes of tail loss in these species (Fleming 1971), and differential rates of loss may have reflected important differences in either predation rates or behaviour between these two species. Indeed, Alberico & Gonzalez-M. (1993) found that *P. semispinosus* was more aggressive than *H. gymnurus*.

Adult male and female *H. gymnurus* were spatially distributed more closely to each other than were the sexes of *P. semispinosus*. This closer association suggested that *H. gymnurus* in the study area may have had a mating system that was different from that of *P. semispinosus* and that was dependent upon its use of widely-separated microhabitats. For instance, Lacher (1981) demonstrated that two sympatric caviid rodents (*Kerodon rupestris* and *Galea spixii*) in northeastern Brazil had different mating systems, which was attributed to differences in microhabitat use. *K. rupestris* was restricted to patches of boulders interspersed among homogenous open thorn scrub and had a polygynous system, while *G. spixii* used the thorn scrub and had a promiscuous mating system. The generalized use of habitat by *P. semispinosus* and broadly overlapping home ranges (Adler *et al*. 1997) suggested that this species had a promiscuous mating system within the study area. However, since a single species of rodent may have various mating systems depending upon environmental characteristics (Wolff 1989), the mating system of *H. gymnurus* may vary from monogamy or polygyny in drier forests with widely-separated riparian microhabitats to a more promiscuous system (similar to that proposed for *P. semispinosus*) in wetter forests where they are not confined to such microhabitats. In these wetter areas, we would expect nearest-neighbour distances of adult males and females to be more comparable to those of *P. semispinosus* observed in this study.

In conclusion, these findings suggest ecological differences between these two echimyids, and we suggest that physiological and behavioural differences may underlie these ecological differences. This study provides a basis for conducting more detailed comparative studies of the demography, behaviour and physiology of *H. gymnurus* and *P. semispinosus*.

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