We examined use of space by adult *Proechimys semispinosus* (Central American spiny rat) on a small island in the Panama Canal using radiotelemetry. The study was conducted with six males and six females during February and March when spiny rats were becoming reproductively active and food resources were scarce. Our study therefore spanned a potentially critical period in which behavioral changes associated with establishment of territories would be most likely to occur. However, home ranges of spiny rats overlapped broadly, and we found no evidence of territoriality. We detected four cases of a male co-occupying a burrow with a female, and one case in which two males co-occupied a burrow. Broadly overlapping home ranges, low nest-site fidelity, and nest-site co-occupancy of single females with more than one male in a short period of time suggested that *P. semispinosus* on this island had a promiscuous mating system. However, the mating system of this species may vary with density, ranging from facultative monogamy at low densities to promiscuity at high densities.

Key words: *Proechimys semispinosus*, spiny rat, home range, spacing patterns, mating system, radiotelemetry, Panama
ulation structure, much as in temperate rodents.

We used radiotelemetry to study use of space and nest sites by a Neotropical forest rodent, *Proechimys semispinosus* (Central American spiny rat), on a small island in the Panama Canal. This frugivorous rodent is a habitat generalist and is often the most abundant rodent in lowland forests throughout its geographic range in Central America and northwestern South America (Adler, 1996). A previous study of spacing patterns within five island populations of *P. semispinosus* showed extensive overlap of home ranges, suggesting that this species does not maintain exclusive territories (Adler et al., 1997). However, that study was based on live-trapping records summed for a 1-year period and may have been too coarse-scaled, both spatially and temporally, to discern finer-scale patterns of space use. Individuals may use space on an exclusive basis over shorter time periods but may shift the position of this defended area over time. For example, spiny rats may defend nest sites or fruit resources within their home ranges. However, because fruit resources in the Neotropics are generally ephemeral, often lasting only a few days, it may be energetically too costly to defend large exclusive territories (Adler et al., 1997). Temporal shifts in spacing patterns therefore may be masked in live-trapping studies that sample individuals over a longer period of time.

We include data collected in the mid-dry season, which is typically a time of low fruit availability on this island (Adler, 1998) and also is the time in which reproductive activity generally begins to increase markedly (Adler and Beatty, 1997). In temperate rodents, the onset of breeding often is accompanied by behavioral changes, primarily increased intraspecific aggression, associated with establishment of territories (Sadler, 1965). If individual *P. semispinosus* defend nest sites or scarce and ephemeral fruit resources, this period in which individuals begin breeding is the time that such aggressive or territorial behaviors are most likely to be manifested. Based on use of space and nest sites, we infer the mating system of individuals within this population.

**Materials and Methods**

Our study was conducted on a 2.7-ha island (Adler, 1994: island 8) in Gatun Lake, which constitutes part of the Panama Canal. The island was covered by tropical moist forest and, compared with other islands in the lake, was characterized by high densities and diversity of tree species that typically produce abundant crops of fruit (Adler, 1998; Adler and Beatty, 1997). This island was separated by 30 m of water from Buena Vista Peninsula, the nearest land mass (Adler and Seamon, 1991). Climate of the study area was highly seasonal, with an 8-month rainy season punctuated by a severe dry season from mid-December through April in which <10% of annual precipitation fell (Windsor, 1990).

We established a 0.8-ha live-trapping grid with 10-m intervals between adjacent traps on the southern third of the island in January 1989. We baited traps with raw corn on 26 January and checked them for 4 days thereafter. Radiocollars (Custom Electronics, Urbana, IL) attached to cable ties with epoxy resin were affixed to 16 adult *P. semispinosus* captured during the 4-day trapping session. Radiocollars weighed 3-4 g, which was ca. 1% of the body weight of each *P. semispinosus*. We used three-element Yagi antennas attached to receivers (AVM Instrument Co., Livermore, CA) to locate collared animals by triangulating from fixed points defined by the grid of trap stations. We triangulated positions of individuals only when they were stationary, as indicated by stability of the radio signal.

Because this species was nocturnal, we conducted telemetry between 1800–0600 h from 2 February to 2 March 1989. To ensure independence of each location, multiple locations of the same individual during a single night were used only if separated by >1.5 h. Diurnal telemetry was conducted from 3 to 18 February to locate nest sites and ascertain burrow occupancy, fidelity, and co-occupancy. When locating those diurnal nest sites, we followed signals to each rat's precise location.

We did not estimate error polygons for our
Table 1.—Home-range characteristics of Proechimys semispinosus on the study island in Panamá.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Number of telemetry locations</th>
<th>Minimum convex polygon area (m²)</th>
<th>Utilization distribution</th>
<th>Number of overlaps with males</th>
<th>Number of overlaps with females</th>
<th>% overlap with males</th>
<th>% overlap with females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>13</td>
<td>666</td>
<td>783</td>
<td>5</td>
<td>1</td>
<td>98</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>2172</td>
<td>709</td>
<td>5</td>
<td>4</td>
<td>96</td>
<td>37</td>
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<tr>
<td></td>
<td>15</td>
<td>840</td>
<td>238</td>
<td>2</td>
<td>2</td>
<td>71</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>959</td>
<td>807</td>
<td>1</td>
<td>2</td>
<td>39</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>633</td>
<td>440</td>
<td>1</td>
<td>1</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>152</td>
<td>461</td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>47</td>
</tr>
<tr>
<td>Male</td>
<td>12</td>
<td>900</td>
<td>1008</td>
<td>3</td>
<td>2</td>
<td>78</td>
<td>59</td>
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<tr>
<td></td>
<td>14</td>
<td>526</td>
<td>273</td>
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<td>10</td>
<td>2401</td>
<td>1501</td>
<td>3</td>
<td>6</td>
<td>9</td>
<td>68</td>
</tr>
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<td></td>
<td>11</td>
<td>1538</td>
<td>657</td>
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<td>5</td>
<td>65</td>
<td>84</td>
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<tr>
<td></td>
<td>11</td>
<td>1196</td>
<td>824</td>
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<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>480</td>
<td>16⁰</td>
<td>3</td>
<td>2</td>
<td>51</td>
<td>23</td>
</tr>
</tbody>
</table>

* Utilization distribution from Fourier method (Anderson, 1982).

These data were used as a predictor of the distribution of home-range use. We compared home-range sizes and overlaps between sexes using t-tests for unequal variances (SAS Institute, Inc., 1990).

RESULTS

All adult males had abdominal testes at first capture and therefore were reproductively inactive. These same individuals at last capture had developed scrotal testes and apparently were reproductively active. Thus, our study spanned the presumably critical period in which reproductive activity commenced and associated behavioral changes would be expected to occur. No trees that produced fruits known to be eaten by spiny rats (Adler, 1995) were fruiting in the study area during our study. We instead observed individuals foraging in leaf litter, apparently for seeds from previous crops of fruits.

We obtained sufficient data for home-range analysis on 12 of 16 individuals to which transmitters were attached (Table 1). Other individuals either left the southern third of the island or their transmitters failed. We inferred that transmitters had no negative effect on the individuals to which...
FIG. 1.—Home ranges of six male and six female *Proechimys semispinosus* from an island population, presented as minimum convex polygons. Symbols represent diurnal nest sites for each individual.

they were attached because body masses increased by an average of 21% for males and 14% for females over period of study.

Mean home-range size did not differ between sexes using estimates from either MCP (males, 1,173 m² ± 723; females, 904 m² ± 678; t = 0.67, P = 0.5206) or UD 50% (males, 713 m² ± 530; females, 573 m² ± 228; t = 0.60, P = 0.5711). There was substantial overlap of home ranges among individuals of both sexes, with a mean of 5.2 individuals occurring within a given convex polygon and a mean overlap of 51% (Fig. 1). That number of individuals occurring within a single home range was an underestimate because we did not affix transmitters to all individuals within the study area. Overlaps between home ranges of females and males were on average larger in area (365 m²) than those between home ranges of females (221 m²) or males (197 m²), although differences were not significant (female-male versus female-female overlap, t = 1.16, d.f. = 16.0, P = 0.2621; female-male versus male-male overlap, t = 1.52, d.f. = 23.0, P = 0.1418; male-male versus female-female overlap, t = 0.2262, d.f. = 10.2, P = 0.8255). Similarly, percentage of overlap did not differ in any of these comparisons (t < 1.08, P > 0.30 for all comparisons).

We detected 19 separate diurnal resting sites (Fig. 1). Most of those sites were underground in burrows, but surface vine tangles and fallen logs also were used. Those locations were distributed widely in the available habitat, from inland forested areas to shoreline banks and debris. Eleven of those diurnal resting sites were used on more than one occasion. We also recorded five instances of co-occupancy involving two females and five males. Four instances involved a male sharing a burrow with a female, and one involved two males sharing a burrow. In one case, a female occupied a burrow with a different male on 2 consecutive days, whereas there was an interval of 2 weeks between co-occupancies involving the other female. The same individuals were not observed together on more than one occasion, but one of the males co-occupied burrows with both females.

**DISCUSSION**

Species of *Proechimys* are widespread and often abundant components of Neotropical rodent communities (Emmons, 1997; Fleming, 1971; Tomblin and Adler, 1998) and have been the subject of several home-range studies (Adler et al., 1997; Emmons, 1982; Fleming, 1971). Results from two of those studies suggested that females exhibited territoriality (Emmons, 1982; Fleming, 1971), but more recent data on *P. semispinosus* suggested that the degree of overlap between individuals may be a function of density rather than an intrinsic trait (Adler et al., 1997). Maximum densities in the studies by Fleming (1971) and Emmons (1982) were <6 spiny rats/ha, while breeding-season densities in the study of five island populations by Adler et al. (1997) were >10 spiny rats/ha. Overlap was low on the lower-density islands but high on the higher-density islands. Such intraspecific flexibility in spacing behavior has been documented in temperate rodents (Ostfeld, 1992; Wolff, 1985).

We found no evidence of territoriality or exclusive use of space by *P. semispinosus* (Fig. 1), consistent with the live-trapping study conducted on the Gatun Lake islands (Adler et al., 1997). Home-range overlap in that study therefore was not simply an ar-
tifact of using longer-term trapping data because we also found coincident use of space in this shorter-term radiotelemetry study. Home ranges of sexes overlapped those of consensuals, although areas of intersexual overlap were greater. We found male-male and male-female co-occupancy of diurnal resting sites. If adult males or females actively defended nest sites, it was unlikely that we would have observed such co-occupancy.

We are unable to address two potentially important aspects of territoriality: defense of nest sites by females with young and defense of locally-clumped ephemeral fruit resources by adults. Our study did not proceed until the first births occurred because the gestation period was 50–60 days (Gliewicz, 1983; Tesh, 1970). It was possible that individuals defended ephemeral fruit resources when such resources began to appear after our study ended. However, broadly overlapping home-ranges, low nest-site fidelity, and nest-site co-occupancy of a single female with more than one male in a short period of time suggest that *P. semispinosus* on this island have a promiscuous mating system. The island in our study has very high densities of *P. semispinosus*, with a maximum reported breeding-season density of 50 spiny rats/ha (Adler, 1998). Individuals in low-density populations where home-ranges do not overlap, such as those studied by Fleming (1971), may be facultatively monogamous if mating opportunities with multiple mates are limited. The possibility that the mating system of *P. semispinosus* may vary with density deserves further study.

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