Kinship, Social Structure, and the Ecological Bases for Sociality in Torch-Tail Spiny Rats, *Trinomys yonenagae* (Rodentia: Echimyidae): Evidence from Field and Molecular Data

by

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Abstract

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Sociality (i.e., group-living) is a multi-dimensional aspect of behavior that occurs in many vertebrate species. Because living in spatially and behaviorally cohesive groups provides the foundation for most forms of complex, cooperative interactions, understanding the reasons for group-living is a fundamental goal for behavioral biologists. In mammals, ecological factors are hypothesized to play a major role in the formation of social groups; the ecological correlates of sociality in individual mammalian species, however, are often poorly understood. The torch-tail spiny rat (*Trinomys yonenagae*) is a South American hystricognath rodent endemic to semiarid sand dunes in northeastern Brazil. *T. yonenagae* is divergent from its congeners in that it is group-living, semi-fossorial, and desert-dwelling; other *Trinomys* species inhabit forests where individuals live aboveground and are solitary. To explore the adaptive bases for these distinctive attributes of *T. yonenagae*, I combined field studies with molecular genetic analyses to (1) characterize the social organization and kin structure of torch-tail spiny rats and (2) identify the primary ecological factors influencing sociality in this species. Most (76.2%) burrow systems monitored were occupied by more than one adult, including same-sex pairs, male-female pairs, and multiple adults of both sexes. Spatial overlap among burrow mates was extensive (72.0 ± 27.0%) and included the use of the same nest site. Kinship among adults decreased as the distance between the burrow systems in which individuals were resident increased. Burrow mates – particularly females – were typically close kin, although unrelated individuals (apparent immigrants from other burrow systems) were also detected within groups. Among adults captured in two successive field seasons, nearly half remained in the same burrow system; among the remaining animals, dispersal was male-biased. Individuals that dispersed to new burrow systems were more related to opposite-sex burrow mates than were individuals that remained in the same burrow system in consecutive years. At the same time, relatedness between dispersers and opposite-sex adults was lower in the new (as compared to the original) burrow system, suggesting that dispersal is related to inbreeding avoidance. Data regarding the distribution of vegetation on the study site revealed that proximity of

food resources to a burrow system was significantly associated with group size. Protective vegetation and number of burrow openings, however, were better predictors of burrow sharing, suggesting that predation is the primary factor shaping social structure in this species. Comparisons of these findings with data from both other echimyids and other desert-dwelling rodent species yield intriguing new insights into the factors favoring sociality among burrow-dwelling rodents.

I dedicate this work to all sertanejos who bravely battle to live in the vast Caatinga.

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Introduction

Rodents, like other vertebrates, include some lineages that are characterized as group-living, meaning that multiple adults spend their lives in close proximity, usually sharing a shelter and nest site (Ebensperger 1998). Hypotheses currently put forth to explain the evolution of sociality in these animals propose a balance between the fitness costs (e.g., parasite transmission, competition for food and mates, infanticide) and benefits (e.g., foraging efficiency, communal burrow digging, reduction in predation risk) of living together (Emlen 1995). These costs and benefits interact to determine group size, composition, and cohesion, which ultimately lead to the expression of a continuum of degrees of the sociality (Lacey and Sherman 2005). Under this conceptual framework, groups may form because the fitness benefits of living with conspecifics outweigh those of living alone (i.e., benefits of philopatry arguments) or because ecological conditions effectively negate dispersing and breeding on one's own (i.e., ecological constraints arguments) (Mumme 1997). Under the latter scenario, living in a group may appear to entail a direct fitness cost, although the low probability of successfully breeding alone should render the net benefits of group-living greater than those of solitary living (Ebensperger 1998).

The studies that have contributed most substantially to our understanding of group-living in rodents have focused on relatively few taxa, notably African mole-rats (e.g., Faulkes et al. 1997, Jarvis et al. 1994) and North American sciurids (e.g., Armitage 1999, Hoogland 1995, Hoogland et al. 1981). As these studies illustrate, determining the adaptive bases for group-living requires knowledge regarding the composition of groups, notably the patterns of kinship among group members. At the same time, basic data regarding patterns of demography and reproductive success can yield important insights into the reasons for sociality. Finally, while efforts to link group-living to specific ecological factors have proven successful for some taxa (e.g., African mole-rats; Jarvis et al. 1994), few comprehensive studies of the ecology of group-living have been completed for rodents (Lacey and Sherman 2007). Thus, while group-living remains a basic attribute of many rodent species, multiple aspects of this phenomenon remain poorly known for many species.

The Echimyidae are a diverse group of Neotropical Hystricognath rodents (Leite and Patton 2002, Galewski et al. 2005). As a lineage, echimyids have experienced an impressive evolutionary radiation in Central and South America, reflected not only taxonomically (ca. 80 species) and biogeographically (echimyids occur in tropical habitats from Central America to Argentina), but also ecologically; these animals occupy semi-aquatic (e.g., *Myocastor*), fossorial (e.g., *Clyomys*), arboreal (e.g., *Echimys*), and terrestrial (e.g., *Proechimys*) niches (Fonseca et al. 1996, Galewski et al. 2005). Although echimyids are typically associated with mesic environments in the Amazon and Brazilian Atlantic forests, a few species (*Carterodon sulcidens*, *Clyomys* spp, *Trinomys yonenagae*, *Trinomys albispinus*, and *Thrichomys apereoides*) diverge from this general pattern and occur in open, drier habitats.

Perhaps associated with this ecological variation, echimyids also display marked divergence in social behavior. While most echimyids are solitary, the coypu (*Myocastor coypus*) and the torch-tail spiny rat (*Trinomys yonenagae*) are group-living (Guichón et

al. 2003, Rocha 1991, Santos 2004). The latter species is semi-fossorial and lives in groups in a sand dune habitat in the semiarid northeastern Brazil (Rocha 1991, 1995). In addition to this behavioral divergence from most echimyids, *T. yonenagae* is morphologically divergent from other extant *Trinomys* but morphologically convergent with distantly related desert-dwelling rodents (Rocha 1995). Thus, *T. yonenangae* appears to provide an ideal species in which to investigate simultaneously the evolution of divergent and convergent adaptations to desert environments, including adaptive patterns of social behavior.

Our current knowledge of the ecology and behavior of echimyids and, more specifically, *T. yonenagae*, is largely anecdotal. As a result, comparative analyses of the ecological correlates of social structure in these animals are challenging (Lacher 1982). To begin to redress this problem, my dissertation research characterizes the social structure and ecology of *T. yonenagae*. Specifically, my work seeks to demonstrate the extent to which this species is social, to characterize the kin structure of groups, and to relate those patterns of genetic kinship to individual movements. In addition, I explore relationships between food distribution, predator protection, and several measures of social structure to identify potential ecological correlates of group-living in this species. By generating these data, I seek to place *T. yonenagae* in the broader comparative contexts of evolutionary divergence within *Trinomys*, as well as evolutionary convergence among multiple lineages of desert-dwelling rodents.

Chapter 1 combines live trapping and radiotelemetry data collected from free-living *T. yonenagae* to provide the first direct, quantitative evidence that this species is social. While previous studies (Rocha 1991, Santos 2004) have suggested that adults of this species can share a burrow systems, these analyses were based upon only indirect evidence of burrow occupancy obtained from localities at which individuals were captured. In this chapter, I describe a novel trapping protocol that limits captures to the individuals resident in a burrow system. At the same time, I use radiotelemetry data collected during daylight hours (while the animals are less active) to examine patterns of spatial overlap and potential nest sharing by adults. Collectively, these analyses indicate that most (~ 76%) of the burrow systems monitored were occupied by multiple adults, confirming that this species is group-living and that adults share subterranean nest sites.

Chapter 2 examines the ecological correlates of sociality in torch-tail spiny rats. Specifically, this chapter seeks to determine which of two key environmental factors – food resources or predator protection – exerts greater influence on the tendency for adult *T. yonenagae* to share burrows. To explore this theme quantitatively, I combine trapping data with data on the distribution of two plant species. While araçá trees (*Eugenia* sp. nov.) represent the primary food resource for *T. yonenagae*, the spiny bromeliad macambira (*Bromelia antiacantha*) is thought to be a critical form of predator protection for these animals. By comparing the distributions of these plant species to several measures of group structure, I demonstrate that although close proximity of food resources influences group size, predator protection appears to be a more important determinant of burrow sharing by *T. yonenagae*. Although these findings support current hypotheses that argue that predation is an important predictor of group-living in rodents, they also reveal that sociality is a multi-dimensional trait that is influenced by numerous interacting ecological factors.

Chapter 3 moves from the field to the lab to characterize the kin structure of *T. yonenagae*. Using microsatellite loci developed as part of this project, I quantify kinship among adults that share a burrow system. I also examine how genetic kinship varies as a function of the distance between the burrow systems occupied by multiple of adults. These analyses reveal that adult burrow mates, particularly females, are typically close kin. Adults of both sexes dispersed to new burrow systems between field seasons; dispersing adults were on average less related to opposite-sex individuals in the new burrow system than they were to opposite-sex adults in their original burrow system, suggesting that individual movement and kin structure may be influenced by inbreeding avoidance.

Chapter 4 integrates the findings of the previous chapters to present a synthesis of our current knowledge regarding the socioecology of *T. yonenagae*. I identify several promising directions for future research on this species and conclude by emphasizing the seminal contributions of the findings presented here to conservation efforts regarding this threatened species, and the unique dune habitat in which it occurs.

Chapter 1

Burrow sharing in the desert-adapted torch-tail spiny rat, *Trinomys yonenagae* (Echimyidae)

Abstract

Among fossorial rodents, burrow sharing is an important behavioral attribute that provides the foundation for multiple aspects of social structure. Within the family Echimyidae, the torch-tail spiny rat (*Trinomys yonenagae*) is distinguished from closely related taxa by its tendency to live in burrows in desert habitats. Preliminary field studies have suggested that burrow systems of this species are shared by multiple adults. To test this hypothesis, I used live-trapping and radiotelemetry to quantify patterns of burrow use in a population of torch-tail spiny rats located near Ibiraba, Bahia State, Brazil. My data indicate that 76.2% of 67 burrow systems monitored were occupied by more than 1 adult, including same-sex pairs, male-female pairs, and multiple adults of both sexes. Spatial overlap among adults captured in the same cluster of burrow entrances was extensive (72.0 ± 27.0% based on 95% minimum convex polygons), with 66.7% of animals resident in the same burrow system using the same putative nest site. Collectively, these data indicate that adult *T. yonenagae* share burrows, suggesting that these animals exhibit a high degree of sociality, unusual for desert rodents and among echimyids. To place these findings in a comparative context and to identify potential ecological correlates of burrow sharing in *T. yonenagae*, I contrast these findings with data on space use by other fossorial, desert-dwelling rodents.

Introduction

Whether animals live alone or in groups is a fundamental distinction that has profound implications for multiple aspects of social behavior, including the occurrence of complex forms of cooperation (e.g., alloparental care; Emlen 1991, Solomon and French 1997) and conflict (e.g., reproductive skew; Clutton-Brock 1989, Vehrencamp 1983). Although animal groups vary widely with respect to attributes such as size, kin structure, breeding composition, and adaptive value (Alexander 1974, Bennett and Faulkes 2000, Busher 2007, Hare and Murie 2007, Koenig and Dickinson 2004, Lacey and Ebensperger 2007), all tend to be characterized by extensive spatial overlap among group members. Among fossorial rodents, such overlap typically includes burrow sharing, in which multiple adults of one or both sexes use the same system of subterranean tunnels and share a common subterranean nest site (Armitage 2007, Ebensperger et al. 2006, Hayes 2000, Lacey 2000, Lacey and Ebensperger 2007, Lacey and Wieczorek 2003, Nevo 1979, Schradin et al. 2006). As a result, burrow sharing - generally thought to be rare among fossorial rodents (e.g., Nevo 1979, Michener 1983, Randall 2007) - offers important clues regarding social structure, including the probability that a species is group-living.

Studies of evolutionary convergence provide important opportunities to test the general applicability of ecological or other hypotheses proposed to explain phenotypic variation, including variation in social behavior (Ebensperger 2001, Ebensperger and Cofré 2001). The spiny rats of the genus *Trinomys* (Rodentia: Echimyidae) represent a little-known example of phenotypic convergence among burrow-dwelling rodents from desert habitats. Within *Trinomys*, the torch-tail spiny rat (*T. yonenagae*) is distinguished by its geographic distribution, ecology, and morphology. While other members of this genus occur in the coastal Atlantic forest and mesic woodlands of Brazil (Lara and Patton 2000), *T. yonenagae* inhabits semiarid sand dunes in the interior of northeastern Brazil (Rocha 1995). Unlike its generally surface-dwelling congeners, *T. yonenagae* is fossorial and displays a morphology that is remarkably convergent with other desert-adapted, burrow-dwelling rodents such as kangaroo rats (*Dipodomys*) and red vizcacha rats (*Tympanoctomys barrerae*). In particular, *T. yonenagae* is characterized by the elongated hind feet and tail, shortened forelimbs, and enlarged auditory bullae characteristic of saltatorial desert taxa (Rocha 1995, Rocha et al. 2007).

Given its apparent convergence with other desert-dwelling rodents, *T. yonenagae* is an important target for studies of interactions between life history (e.g., ecological relationships) and phenotype, including ecological determinants of social structure. Preliminary field studies indicate that multiple adult torch-tail spiny rats can be captured in the same burrow system (Rocha 1995), suggesting that *T. yonenagae* is group-living. To date, however, no quantitative studies of burrow or nest sharing by free-living adults have been conducted for this species. As a first step toward identifying the ecological factors influencing social behavior in these animals, I characterized patterns of space use by adult *T. yonenagae*. Specifically, I tested the hypothesis that adults share burrow systems and putative nest sites. In addition to providing the first quantitative data regarding space use by free-living members of this species, our analyses facilitate efforts to place torch-tail spiny rats within the comparative behavioral framework offered by semi-fossorial desert species, thereby guiding future efforts to identify the ecological correlates of space use and social structure in *T. yonenagae*.

Materials and Methods

Study area

The 5.6 ha study site encompassed 3 parallel sand dunes located along the left bank of the Rio São Francisco, 0.5 km NE of the village of Ibiraba in Bahia State, Brazil (10°47'S, 42°49'W; Figure 1-1). The majority (> 75%) of burrow systems used by the study animals were located on the valley floors between dunes (Santos 2004). Vegetation in the valleys was sparse (~ 50% bare ground; Rocha et al. 2004), resulting in high soil temperatures (~ 60°C) during the day. The herbaceous vegetation consisted primarily of the spiny bromeliad *Bromelia antiacantha* and the small cactus *Tacinga inamoena*. Members of the genus *Eugenia* (Myrtaceae) represented 34.1 % of all tree and shrub species (Rocha et al. 2004); their seeds provided most of the food and water consumed by *T. yonenagae* (Santos 2004).

The study site was characterized by a semiarid climate, with highly seasonal and unpredictable precipitation (annual range = 400-800 mm; Bahia-Seplantec 1978). The rainy season occurred from October to March, with the dry season extending from April to September (Nimer 1979). Data for this study were collected from June to August in 2005-2008. Specifically, field work was conducted for 40 days in 2005, 45 days in 2006, 35 days in 2007, and 25 days in 2008. During data collection, ambient temperatures ranged from 15°C at night to 43°C during the day.

Animal capture

Active burrow systems were identified by the presence of freshly excavated soil at burrow entrances, footprints of spiny rats in fresh mounds of soil, and remains of recently eaten *Eugenia* seeds around burrow entrances. Preliminary trapping efforts revealed that the mean distance between recaptures of the same individual was 5.5 ± 3.5 m (range: 0.7-14 m; $n = 36$ recaptures) (Santos, unpubl. data). As a result, I initially assigned burrow entrances located $\leq$ 15 m apart to the same burrow system; burrow entrances > 15 m apart (i.e., more than 2 times the mean distance between recaptures) were assigned to different systems. As part of the current study, I used capture locations and telemetry to confirm that burrow entrances assigned to the same cluster were indeed part of the same system. All capture locations were recorded by determining the compass direction and distance of the burrow entrance from a fixed, georeferenced stake placed in the center of each burrow system. I converted each capture locality to x and y values that were plotted on a Cartesian coordinate system, allowing localities for different animals to be mapped relative to one another.

To characterize the animals occupying each burrow system, I attempted to capture all members of the study population each year using locally made 30 × 15 × 15 cm live traps constructed of wire mesh and baited with small slices of squash. Squash was used as bait because other baits tested attracted ants, which usually killed trapped torch-tail spiny rats (Rocha 1991). Because *T. yonenagae* is nocturnal, traps were set in the afternoon (1600 h) and closed the following morning (0600 h). To ensure that only animals using a given burrow system were captured, trap entrances were fitted with a 50 × 30 cm canvas sleeve, the other end of which was attached to a 20 cm long piece of PVC plumbing pipe (12 cm

diameter). The open end of the PVC tube was placed in an active burrow entrance. Because the diameter of the tube was slightly greater than most burrow entrances, it was necessary to insert the tube into the soil, providing a tight seal around the focal burrow entrance. As a result, only spiny rats that exited the system via the focal burrow opening could enter the trap, thereby preventing individuals from other systems (i.e., animals traveling above ground) from being captured. Traps were set simultaneously at all burrow entrances thought to belong to the same system, as determined by proximity and evidence of recent activity (see above). Individuals were considered residents when captured repeatedly (more than twice) within the same cluster of burrow entrances.

To ensure that all animals resident in a burrow system were trapped, each individual captured was placed in a standard polycarbonate rodent cage (dimensions: 40 × 40 × 15 cm), with only individuals trapped in the same cluster of burrow entrances housed in the same cage (≤ 3 adults per cage). Cage bottoms were lined with a 2 cm layer of dry sand; wet or soiled sand was replaced daily. Captured animals were maintained in a separate room within the building used to house researchers. While in captivity, the animals were provided with fresh water and were fed squash and fruits *ad libitum*. Trapping of a given burrow system continued until no animals had been captured and no activity had been detected at burrow entrances for 48 h (Lacey et al. 1997). Once trapping was complete, all animals held in cages were released at the point of capture.

Marking and tissue sample collection

For all individuals captured, I recorded body weight to the nearest gram (300 g Pesola® spring scale), sex, and apparent reproductive status. For females, reproductive condition was determined by visual inspection of the external genitalia (e.g., perforate vagina) and mammae (e.g., enlarged teats characteristic of lactation) and by palpation of the abdomen (for presence of embryos). Because the testes of males of this species never descend and because *T. yonenagae* displays no sexual dimorphism in body size, male reproductive status was determined based on body weight. Specifically, because all reproductively active females weighed ≥ 90 g, I assumed that males weighing ≥ 90 g were also reproductively mature adults (Santos 2004).

Just before their release, newly captured animals were lightly anesthetized with Isoflurane (Halocarbon Industries, Eagle River, New Jersey), after which they were marked with a uniquely numbered metal ear tag (Monel # 1005-1, National Band and Tag Company, Newport, Kentucky) applied to 1 ear. A small tissue sample (~ 2 mm of the distal end of one pinna) was collected as part of ongoing studies of kinship and parentage in the study population, the results of which are reported elsewhere. Following recovery from the anesthesia, each individual was released into the burrow entrance at which it had been captured.

Radiotelemetry

During the 2006 to 2008 field seasons, I used radiotelemetry to quantify space use and nest sharing by adults in the study population. Radiotransmitters (model BD-2C, Holohil Systems Ltd., Carp, Ontario, Canada) were attached to the animals using a wire collar that was sheathed in silicon tubing to minimize risk of injury. Collar weight (2.0 g) did not exceed 2.0 % of mean adult body mass (130.5 ± 19.1 g, n = 238 animals) and had no apparent impact on the behavior of the study animals. Because the number of

transmitters available for use was limited, no more than 3 adults per putative burrow system were fitted with radiocollars. Although *T. yonenagae* is nocturnal, I was particularly interested in determining whether adults shared burrow systems and nest sites and thus I recorded fixes (i.e. location of the strongest signal for a radiocollared individual) during the daytime (0600-1200 h and 1500-1700 h) when the animals were most likely to be underground.

To locate radiocollared animals, I used a digital telemetry receiver (model R-1000, Communication Specialists, Inc., Orange, California) and a 3-element hand-held Yagi antenna. Once the signal for an individual had been detected, I quietly walked towards the signal until its amplitude indicated that I was standing directly over the animal. Based on fixes recorded for transmitters buried at known locations, I found this procedure to be accurate to 0.5 m. For each animal located via telemetry, I took 3 fixes of its position before placing a flag labeled with the animal ID number and date and time of the fix at the point where the strongest signal was detected. At least 30 min were allowed between successive fixes of the same animal; preliminary telemetry data indicated that individuals were rarely in the same location after 30 mins, suggesting that this interval was sufficient to minimize potential temporal dependence of successive data points (Swihart and Slade 1997). Radiotracking continued for 4-5 days, after which the locations of fixes were recorded by measuring the compass angle and distance (m) of each flag from the same fixed reference point used to map capture sites (Lacey et al. 1997). At the end of each field season, radiocollared adults were recaptured and their collars were removed.

All field procedures followed institutional guidelines and the guidelines of the American Society of Mammalogists (Gannon et al. 2007). The study was conducted under permits issued by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA # 0123475 BR, #10959-1).

Analyses of spatial data

To characterize space use by members of the study population, the location of each radio fix was transformed into Cartesian coordinates (Lacey et al. 1998). To characterize space use, a 95% minimum convex polygon (MCP) was generated for each radiocollared individual using the Animal Movement extension of ArcView GIS 3.2 (ESRI Technology). MCPs were employed to facilitate comparisons between our data and results obtained from other rodent species (e.g., Ribble et al. 2002, Seamon and Adler 1999); 95% rather than 100% MCPs were used because the former are somewhat more conservative with respect to estimates of spatial overlap among individuals. Pairwise calculations of the percentage overlap between individuals were completed using ArcGIS 9.0 software package (ESRI, Redlands, California). To determine whether adults shared nests, I identified the putative nest for each radiocollared animal as the location most frequently used by that individual. Given the accuracy of our telemetry data, all fixes located within a radius of 0.7 m of one another were treated as the same location.

To characterize the individuals sharing a putative burrow system, I identified all adults that were captured in the same cluster of burrow entrances during the same field season. These data were compared to patterns of overlap for 95% MCPs to determine if individuals captured in the same putative burrow system were spatially distinct from animals captured in other clusters of burrow entrances. Using these data, I then

determined the number of adults of each sex associated with the same putative burrow system.

Statistical analyses

Parametric statistical tests were used for data that met the associated assumptions. To determine whether the number of fixes per individual influenced our spatial analyses, I used correlation analysis to examine the relationship between number of fixes and size of area used (95% MCP) for 6 randomly chosen radiocollared adults (n = 2 per year). Analysis of variance (ANOVA) was used to examine home range size and percentage overlap for 95% MCPs as a function of sex and year, with percentages arcsine transformed prior to analysis. A Mann-Whitney U test was used to compare the degree of spatial overlap among adults captured in the same cluster of burrow entrances (i.e. burrow mates) to the degree of overlap among animals captured in distinct clusters of entrances (i.e. non-burrow mates). Statistical analyses were performed using JMP 7.0.2 (SAS Institute Inc., 2009). Means are reported ± 1 *SD* with statistical significance set at $\alpha = 0.05$. All statistical tests were 2-tailed unless otherwise noted.

Results

A total of 180 adult (95 male, 85 female) and 66 juvenile (29 male, 37 female) *T. yonenagae* were captured during this study. Only 31 (17.2%) of these adults were recaptured in the same burrow system in successive years; no more than 1 adult per burrow system was recaptured in different years. As a result, I considered data from each field season to be independent for the purposes of characterizing burrow use.

Based on the locations of active burrow entrances, the study site contained a mean of 54.8 ± 8.8 (range = 42-60) occupied burrow systems per year (Table 1-1). The increase in number of burrow systems per year over the course of the study was due primarily to the presence of newly occupied burrows on the study site in each successive year. When all clusters of burrow entrances (active and inactive) were considered, the mean percentage of burrow systems occupied per year was 55.5 ± 14.2% (n = 4 years); the mean annual density of occupied burrow systems was 9.9 ± 1.6 systems/ha (Table 1-1). Based on the locations of burrow entrances assigned to the same system, the area encompassed by individual burrow systems ranged from 4 to 320 m^2; because the subterranean portions of these systems were not quantified, however, these values may not provide robust estimates of the actual sizes of individual burrow systems. When data from all years were considered, the mean distance between the spatial centers of adjacent burrow systems (as determined from the locations of burrow entrances) was 22.6 ± 7.3 m (range = 8.4-41.7 m, n = 100 pairwise comparisons of adjacent systems). The number of burrow entrances per system ranged from 1-13 (mean = 5.4 ± 4.2 entrances/system, n = 219 systems).

Analyses of burrow use

Of 34 adults fitted with radiocollars, 3 disappeared from the study population and 2 moved to a different burrow system during the course of data collection. An additional 2 radios failed before data collection was completed. As a result, analyses of space use were based on radio fixes from 27 individuals (2006: 6 males, 5 females; 2007: 5 males,

5 females; 2008: 4 males, 2 females). Telemetry data collected over 4 to 5 consecutive days yielded a minimum of 33 fixes per individual (2006: 48.1 ± 4.2 fixes/individual, n = 11 adults; 2007: 50.2 ± 3.9 fixes/individual, n = 10 adults; 2008: 59.7 ± 5.4 fixes/individual, n = 6 adults).

The number of fixes per individual was significantly correlated with 95% MCP size for each of the 6 randomly selected individuals examined (all r values ≥ 0.60, all P < 0.0001, Bonferroni corrected $\alpha = 0.008$). In all cases, however, the relationship between number of fixes and cumulative 95% MCP size reached a plateau at ≤ 35 fixes per individual (2006: ≤ 27 fixes; 2007: ≤ 29 fixes; 2008: ≤ 35 fixes), suggesting that the mean number of fixes per animal obtained during this study provided a reliable estimate of the burrow area used by an individual. Changing the interval between fixes appeared to have no effect on estimates of the area used by an individual; resampling of the data set revealed no significant differences in size between 95% MCPs calculated for the same individual using 30 min versus 60 min inter-fix intervals (n = 19 individuals, Student's t test: t_{36} = - 0.259, P = 0.79). Although these analyses do not preclude temporal autocorrelation among telemetry fixes for the same individual, they suggest that our analyses of space use were not substantially influenced by the interval between fixes.

When all radiocollared animals were considered, the sizes of 95% MCPs did not differ with sex (males: 5.63 ± 4.40 m^2, n = 15, females: 6.68 ± 4.90 m^2, n = 12) or year (2006: 4.42 ± 4.09 m^2, n = 11; 2007: 8.49 ± 4.98 m^2, n = 10; 2008: 5.16 ± 3.43 m^2, n = 6) (ANOVA: $F_{2, 27}$ = 2.487, P = 0.10). When data from all individuals were pooled, the mean size of 95% MCPs was 6.36 ± 4.44 m^2 (range = 0.55-15.81 m^2, n = 27 adults).

Evidence of burrow sharing

Few burrow systems were trapped completely (i.e., all animals captured) in 2008 and thus this year was not included in analyses of burrow sharing and occupancy. During the 2005 to 2007 field seasons, all adults (n = 156) resident in 88 burrow systems were captured; 121 (77.6%) of these animals were caught at more than 1 burrow entrance. In all cases, capture localities for the same individual were located within the same cluster of burrow entrances. Based on these data, I assigned animals captured within the same cluster of burrow entrances to the same burrow system.

Analyses of 95% MCPs revealed that adults captured in the same burrow system displayed extensive spatial overlap with one another. The percentage overlap between 95% MCPs for adults captured in the same burrow system did not differ between years (2006: 66.3 ± 29.2%, n = 20 pairs of burrow mates; 2007: 83.4 ± 20.4%, n = 10; 2008: 72.2 ± 23.3%, n = 6; ANOVA: $F_{2, 36}$ = 1.282, P = 0.19) or with the sex(es) of the individuals compared (male-male: 72.9 ± 23.9%, n = 10 pairs of burrow mates; female-female: 72.9 ± 44.7%, n = 4; male-female: 71.4 ± 25.4%, n = 22; ANOVA: $F_{2, 36}$ = 0.0119, P = 0.87) and thus data from all burrow mates were pooled for subsequent analyses. Based on this pooled data set, the mean overlap between 95% MCPs for burrow mates was 70.0 ± 27.1% (n = 36 pairs of burrow mates); in contrast, no overlap was detected between 95% MCPs for the 36 pairs of non-burrow mates for which telemetry data were available. This difference in percent overlap was significant (Mann-Whitney $U_{2, 36}$ = 7.87, P < .0001), suggesting that individuals only overlapped spatially with burrow mates.

On average, the single most frequently recorded location for an animal represented 56.4 ± 23.7 % of the total number of fixes for that individual (n = 27 adults). In contrast, the 2nd most frequently recorded location represented only 18.6 ± 6.5% of the total number of fixes per individual; this difference was significant (Wilcoxon signed-rank test: $Z_1 = -4.829$, $P < .0001$). Because telemetry data were recorded during the daytime when the study animals were largely inactive, I assumed that the most common fix locality for each adult represented that individual's nest site (Figure 1-2). For individuals assigned to the same burrow system, 18 (66.7%) of 27 burrow mates shared the same putative nest site. Overall, the mean distance between putative nest sites was 0.84 ± 0.41 m (n = 27 pairs of burrow mates); in comparison, the mean distance between putative nests for adults resident in different burrow systems was 56.0 ± 40.9 m (n = 10 randomly selected pairs of nearest-neighbor nests). Collectively, these data demonstrate that adults in the study population shared burrow systems and, in some cases, apparent nest sites.

Characterization of burrow occupancy

More than 1 adult was captured at 233 (64.4%) of the 362 burrow entrances at which traps were set during this study. Adults in 12 of these systems were also monitored via telemetry; in all cases, telemetry data confirmed that the individuals captured in a given cluster of burrow entrances were resident in that burrow system. Across years (2005 to 2007), the majority of burrow systems (76.1 ± 2.7%; n = 67) were occupied by ≥ 2 adults (Table 2-1). The number of individuals captured ranged from 2 to 5 adults (2.9 ± 1.3) and 0 to 4 (1.7 ± 0.48) juveniles per burrow system. Burrow systems occupied by male-female pairs or multiple adult males (no females) were most common, although burrow systems occupied by multiple females (no males) and by multiple adults of both sexes were also encountered (Table 2-1). Twenty burrow systems contained multiple adult females; in 7 (35%) of these systems, more than 1 female was reproductively active, suggesting that multiple adult females can breed while occupying the same burrow system.

Discussion

My data indicate that free-living adult *T. yonenagae* share burrow systems and, in some cases, putative nest sites. In my study population, multiple adults were captured in more than 75% of the burrow systems monitored. Adults captured within the same cluster of burrow entrances exhibited substantial spatial overlap, while individuals captured in different clusters never overlapped spatially with one another. Individuals occupying the same cluster of burrow entrances also typically shared the same putative nest site. Collectively, these findings suggest that *T. yonenagae* meets both spatial criteria – burrow sharing and nest sharing – typically used to diagnose sociality in fossorial rodents (Lacey 2000, Urrejola et al. 2007). While additional research is needed to characterize the social structure (e.g., patterns of kinship among burrow mates) of *T. yonenagae* in detail, my data are consistent with previous studies that have reported high rates of affiliative behavior among captive adult torch-tail spiny rats (Freitas et al. 2008, 2010) and provide the 1st quantitative evidence of group-living among free-living members of this species.

The number and sex(es) of the animals occupying burrow systems varied markedly within the study population. Adults sharing the same burrow system included same-sex pairs, male-female pairs, and groups of 3 or more adults of both sexes. This variation in group composition resembles that reported for other species of desert-dwelling rodents such as *Meriones unguiculatus* (Ågren et al. 1989), *Rhabdomys pumilio* (Schradin and Pillay 2004), and *Rhombomys opimus* (Randall et al. 2005). Randall et al. (2005) have argued that this type of flexible social structure is an adaptive response by members of desert species that must cope with harsh and unpredictable environments. More specifically, as ecological conditions in desert habitats change, animals may shift between living alone and living in groups to maintain the social setting that is most adaptive for a given set of environmental conditions. The dune habitat in which *T. yonenagae* lives varies temporally with respect to factors such as rainfall and food availability (Rocha et al. 2004, Rocha and Rodrigues 2005), suggesting that variation in burrow occupancy in this species may also reflect adaptive responses to variable environments.

Although is possible that the patters of burrow occupancy revealed in this study were under influence of seasonal conditions related to the sampling period (i.e., the dry season), previous studies in this area indicated that proportions of social groups their social structure was not significantly affected by seasonality (see Chapter 2).

Ecology of burrow sharing in *T. yonenagae*

Three ecological factors that are frequently identified as promoting sociality are food resources, predation, and thermoregulatory requirements (Alexander 1974, Ebensperger 2001). Although the ecology of *T. yonenagae* has not been well characterized, both the patchy spatial distribution and variable temporal production of *Eugenia* seeds that this species consumes suggest that availability of food resources and, in particular, the formation of food caches (Santos 2004) may be an important component of burrow sharing in this species. No quantitative studies of predation have been conducted for *T. yonenagae* but these animals are the only small mammals found in the dunes near Ibiraba (Rocha 1995) and are thus likely to be the primary prey item for multiple predators. *T. yonenagae* appears to evade most predators by darting into burrows, suggesting that these structures are an important source of predator protection (Ebensperger and Blumstein 2006, Ebensperger and Wallem 2002, Hayes et al. 2007). Burrow systems may also function as refugia from the extreme heat and aridity of the environment in which *T. yonenagae* occurs (Rocha 1991). Construction of subterranean burrows is thought to be energetically expensive (Ebensperger and Bozinovic 2000, White et al. 2006) and burrow sharing may allow individuals to reduce the costs associated with access to this critical resource. Future studies will evaluate these potential ecological influences on burrow sharing by *T. yonenagae* in greater detail.

Comparisons with other echimyids

Spiny rats in the genus *Trinomys* are primarily forest-dwelling animals that lack conspicuous morphological adaptations for specialized forms of locomotion. *T. yonenagae* differs from other echimyids – including other species of *Trinomys* – in numerous ways, including morphology (e.g., elongated hind limbs and tail; Rocha 1995), mode of locomotion (e.g., saltatorial movement associated with sandy habitats; Rocha et

al. 2007), and reliance on subterranean burrows (fossoriality; Mares 1980). Although other echimyids generally have been assumed to be solitary (e.g., *Trinomys*: Bergallo 1994, 1995; *Proechimys*: Aguilera 1999, Emmons 1982; *Thrichomys*: Streilein 1982), several recent studies suggest that the social systems of these animals may be more complex than previously realized. For example, home ranges of adult Tome's spiny rats (*P. semispinosus*) have been shown to overlap extensively, with males and females sharing nest sites on a short-term basis (Endries and Adler 2005, Seamon and Adler 1999). The arboreal southern bamboo rat (*Kannabateomys amblyonyx*) appears to change its mating system from social monogamy to polygyny in response to the distribution of food resources (Silva et al. 2008). Finally, both field (Guichón et al. 2003) and molecular analyses (Túnez et al. 2009) indicate that the semi-aquatic coypu (*Myocastor coypus*) lives in groups composed of multiple adults of both sexes. Collectively, these studies suggest that some degree of sociality may be more common among echimyids than has typically been assumed, with the result that group-living in *T. yonenagae* may not represent a marked contrast to other members of this family.

Comparisons with other desert rodents

Because *T. yonenagae* shares a number of phenotypic attributes with other burrow-dwelling rodents from arid habitats (Rocha 1995, Rocha et al. 2007), comparative studies of these taxa may yield important insights into the ecological bases for group-living in desert species. Other arid-adapted rodents are known to engage in burrow sharing (e.g., *R. opimus*: Randall et al. 2005; *M. unguiculatus*: Ågren et al. 1989; *Notomys alexis*: Watts and Aslin 1981), providing the opportunity to use convergent patterns of social structure to generate robust tests of ecological hypotheses for group-living (Ebensperger 2001, Ebensperger and Cofré 2001). Future studies of torch-tail spiny rats will exploit this framework to explore the effects of food resources, predation, and thermoregulation on the tendency to live in groups. In addition to clarifying the ecological bases for burrow sharing in *T. yonenagae*, such studies will facilitate understanding of variation in social structure among all burrow-dwelling desert rodents.

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Table 1-1. Occurrence of burrow systems of *Trinomys yonenagae* on the study site in Brazil. For each year of the study, number and density of burrow systems (occupied and unoccupied) are indicated, with number and percentage of all burrow systems occupied by *T. yonenagae*.

Year	Total number of burrow systems (n)	Density of burrow systems mapped (total/ha)	Occupied burrow systems	
			n	% of total
2005	42	14.4	31	73.8
2006	56	14.8	33	58.9
2007	61	14.9	29	47.5
2008	60	10.4	25	41.7
All 4 years (mean ± *SD*)	54.8 ± 8.8	13.6 ± 2.2	29.5 ± 3.4	55.5 ± 14.2

Table 1-2. Characterization of adult *Trinomys yonenagae* residents in 88 burrow systems monitored in Brazil in 2005-2007. In all cases, all adults resident in the same burrow system during the same field season were captured; data from 2008 are not included due to the limited number of burrow systems from which all animals were trapped. Same sex groups consisted of ≥ 2 adults of the same sex; mixed sex groups consisted of ≥ 3 adults of both sexes.

	Lone adults			Opposite-sex pairs		Same sex groups				Mixed sex groups		Total number
						Males		Females				
Year	Males	Females	% of total	*n*	% of total	*n*	% of total	*n*	% of total	*n*	% of total	of systems
2005	2	5	23.3	8	26.7	8	26.7	5	16.7	2	6.7	30
2006	4	4	26.7	10	33.3	7	23.3	5	16.7	0	0	30
2007	3	3	21.4	7	25.0	7	25.0	5	17.9	3	10.7	28
Total	9	12	23.9	25	28.4	22	25.0	15	17.0	5	5.7	88

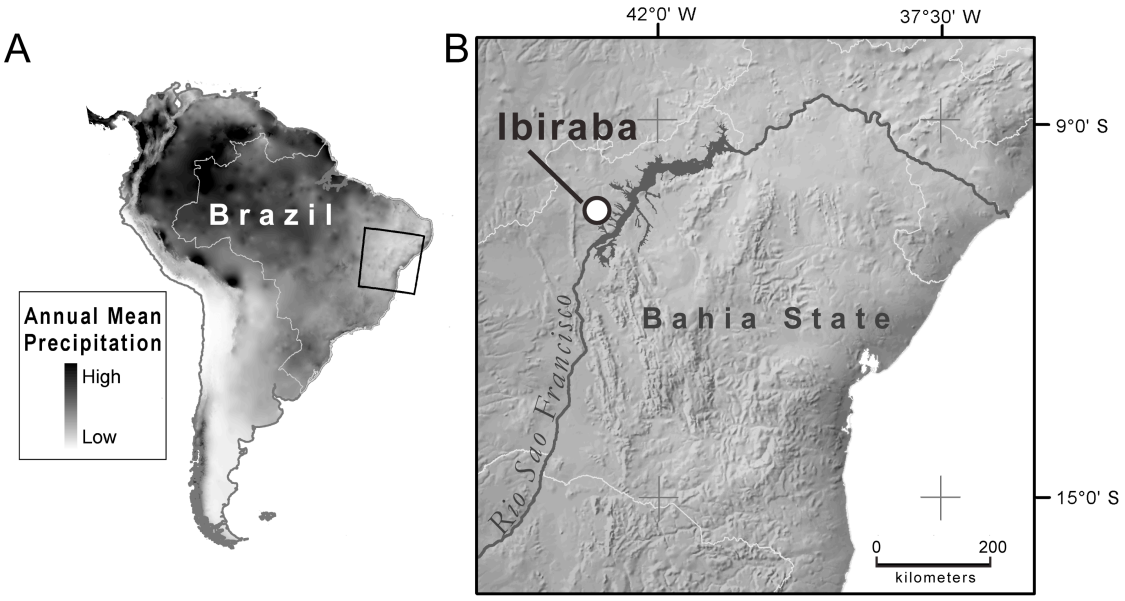

Figure 1-1. Map indicating the location of the study site near Ibiraba, along the Rio São Francisco, Brazil. (A) Precipitation gradient map of South America showing the contrast between high precipitation (dark) and low precipitation areas (light); the semiarid Caatinga habitat in Northeastern Brazil is partially framed by the small rectangle. (B) Detailed map of the study region (area included in the rectangle in A), with the location of the study site for *T. yonenagae* indicated by the white circle.

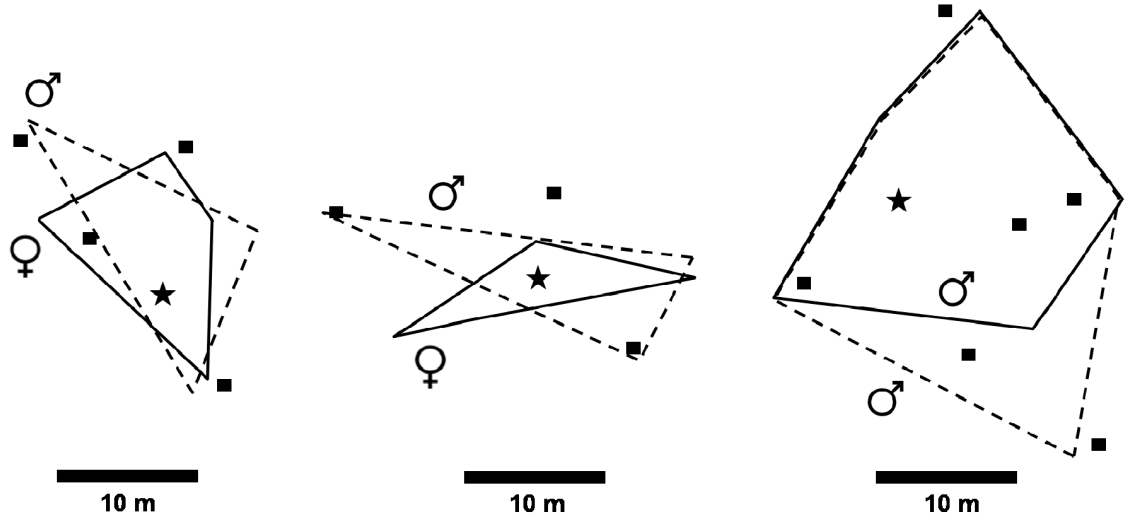

Figure 1-2. Spatial overlap for 6 adult *T. yonenagae* monitored via radiotelemetry during 2008. The animals shown were resident in 3 distinct burrow systems; for each system, the locations of burrow entrances are denoted by squares. For each individual, a 95% MCP was constructed based on radiofixes collected during daylight hours. For each burrow system, the MCP for one animal is denoted with a solid line while the MCP for the other is denoted with a dashed line; the shared putative nest site for each pair of animals is indicated with a star. In all cases, additional adults were resident in each burrow system but were not monitored via telemetry.

Chapter 2

Ecological predictors of sociality in the torch-tail spiny rat, *Trinomys yonenagae* (Echimyidae)

Abstract

Predation risk and the distribution of food resources are thought to influence group-living and social structure in multiple vertebrates. As a first step toward determining if these ecological factors contribute to burrow sharing and social structure in torch-tail spiny rats (*Trinomys yonenagae*), I examined whether protective cover, number of burrow openings, distance to food, and number of food sources (*Eugenia* trees) influenced group size, per capita female fitness, and adult survival in a population of *T. yonenagae* from northeastern Brazil. Degree of protective cover, number of burrow entrances, and number of food resources located within 16 m of a burrow entrance were positively associated with group size, but not with female fitness or adult survival. Additionally, number of burrow openings was positively associated with per capita female direct fitness. These relationships suggest that members of larger groups did not have to travel as far to access critical food resources and had greater protection from potential predators, indicating that the nature of the burrow system may influence social structure in *T. yonenagae*. These findings are used to place the study species within the larger comparative context of the ecology of social structure in *Trinomys* as well as in other, phylogenetically distinct burrow dwelling rodents.

Introduction

Animal social systems range from solitary to highly gregarious; understanding why such variability occurs is a central goal in behavioral ecology. Groups are predicted to form when the fitness benefits of living together outweigh the costs of living gregariously (Alexander 1974, Dunbar 1989). Ecological variables – in particular predation risk and food resource distributions – are thought to be key factors influencing the formation of groups in numerous vertebrates, including fishes (Heg et al. 2004), birds (Beauchamp 1999, Pulliam 1973), and multiple species of mammals (Blundell et al. 2002, Bradbury and Vehrencamp 1977, Brashares and Arcese 2002, Caraco and Wolf 1975, Faulkes et al. 1997, Van Schaik 1983, White 2010). Despite the apparent importance of these ecological parameters in promoting group-living, surprisingly few studies have compared the relative contributions of food and predation to space use and social structure in the same study system (but see Brashares and Arcese 2002, Ebensperger et al. 2009, Hoogland and Sherman 1978, Pitelka et al. 1974). As a result, the interplay between predation risk, food resources, and the tendency to live in groups remains poorly characterized for most group-living species.

The torch-tail spiny rat, *Trinomys yonenagae*, is a semifossorial caviomorph rodent that is endemic to semiarid dune habitat in northeastern Brazil (Rocha 1995). While other *Trinomys* are generally forest dwelling and solitary, the torch-tail spiny rat is a group-living desert dweller (Rocha 1995). *T. yonenagae* exhibits a flexible social structure, with some burrow systems occupied by a single individual and others occupied by groups of 2-5 adults (Santos 2004, Chapter 1). Adults that share a burrow system also tend to share a subterranean nest, where offspring are reared communally (Chapter 1). Groups form primarily due to natal philopatry, with the result that burrow mates – particularly females – are frequently closely related to one another (Chapter 3).

Given the striking difference in social structure between *T. yonenagae* and other species of *Trinomys*, studies of torch-tail spiny rats provide an important opportunity to explore the ecological factors promoting group-living in this genus. The occurrence of *T. yonenagae* appears to be associated with two plant species: araçá-de-boi trees (*Eugenia* sp. n, Myrtaceae) and the spiny bromeliad macambira (*Bromelia antiacantha*, Bromeliaceae) (Rocha 1991, Santos 2004). While the former serves as the primary food resource for *T. yonenagae* (Santos 2004), the latter is thought to provide an important source of cover for the animals, which typically construct their burrow entrances within clumps of macambira (Rocha 1991, Santos 2004).

To examine the effects of these two important resources on the social structure of *T. yonenagae*, I investigated whether the spatial distribution of food (araçá trees) and protection (macambira and burrow openings) was associated with inter-burrow differences in group size, adult survival, and offspring production. Specifically, I predicted that if food resources are critical determinants of social structure then close proximity to araçá trees would be associated with greater numbers of adults per group (i.e., larger groups), enhanced adult survival, and higher offspring production. Similarly, if predator protection influences social structure, then I predicted that group size, female fitness, and adult survival would be positively correlated with number of burrow openings and proximity to spiny vegetation. In addition to providing the first empirical data regarding the ecology of social behavior in this species, this study yields important

new insights into the factors favoring burrow sharing in this member of an otherwise solitary genus of Neotropical rodents.

Materials and Methods

Study area and animals

The 2.88 ha study site was located along the left bank of the Rio São Francisco, approximately 0.5 km NE of the village of Ibiraba in Bahia State, Brazil (Figure 1-1). The study area, which consisted of 3 parallel sand dunes and the intervening valleys, was characterized by a semiarid climate with highly seasonal and unpredictable precipitation (annual range = 400-800 mm; Bahia-Seplantec 1978). The rainy season occurred from December to March, with the dry season extending from April to November. Data for this study were collected during 4 field trips completed during 2000-2001. Specifically, field work was conducted on 16 days in February 2000 (mid wet season), 12 days in June 2000 (early dry season), 13 days in October 2000 (late dry season), and 14 days in January 2001 (early wet season).

The majority (> 78%) of burrow systems used by *T. yonenagae* were located on the valley floors between dune summits (Santos 2004). Vegetation in the valleys was sparse (~ 50% bare ground; Rocha et al. 2004) and herbaceous, consisting mostly of dense clumps of macambira *Bromelia antiacantha* (Bromeliaceae) and the small cactus *Tacinga inamoena*. Members of the genus *Eugenia* (Myrtaceae) represented 34.1 % of all tree and shrub species.

Ecology of *T. yonenagae*

Although the study population of *T. yonenagae* reproduced year round, recruitment rates for juveniles were higher during the mid-late wet season and declined toward the mid-dry season.

The prevalence of *Eugenia* seeds in the diet of torch-tail spiny rats (Santos 2004) and their role as a major water source for these animals (Santos E., 1997) indicate that these trees are a critical food resource for *T. yonenagae*. Accordingly, I expected that proximity to *Eugenia* tress and the abundance of these trees near burrow entrances would provide individual *T. yonenagae* with better (easier, greater) access to food resources. As a result, adults from burrow systems characterized by more *Eugenia* trees and *Eugenia* trees located nearer to burrow entrances would have greater per capita direct fitness, enhanced survival and, consequently, live in larger groups.

No quantitative studies of predation have been conducted for *T. yonenagae*, but because these animals are the only small mammals on the study site (Rocha 1995) they are assumed to be prey for multiple predators, including felids (*Leopardus tigrinus*, *Puma yagouaroundi*), canids (*Cerdocyon thous*), owls (*Athene cunicularia*, *Megascops choliba*, *Tyto alba*), snakes (*Bothrops erythromelas*, *Crotalus durissus*), and lizards (*Tupinanbis teguixin*); sightings of these predators near *T. yonenagae* burrow systems and evidence of spiny rat mortality due to these predators were recorded during almost all field trips. Observations of spiny rat response to potential predatory risk (i.e., human approach) indicated that the animals run into burrow entrances located under spiny vegetation to avoid danger (see also Cassini and Galante 1992, Kinlaw 1999, Longland and Price

1991). As a result, I predicted that animals living in burrow systems characterized by a greater number of burrow entrances and closer proximity to the spiny bromeliad macambira would display greater per capita direct fitness and enhanced survival and, thus, would live in larger groups.

Burrow systems and animal capture

Occupied burrow systems were identified by the presence of freshly excavated soil at burrow entrances, footprints of spiny rats in fresh mounds of soil, and remains of recently eaten *Eugenia* seeds left near burrow entrances. Initially, I identified distinct burrow systems based on the spatial aggregation of burrow entrances. Preliminary trapping efforts revealed that the mean distance between recaptures of the same individual was 5.5 ± 3.5 m (range = 0.7-14 m; n = 36 recaptures). As a result, I assigned burrow entrances located ≤ 15 m apart to the same burrow system; burrow entrances > 15 m apart (i.e., beyond the upper range of distance between recaptures) were assigned to different systems (Chapter 1).

To characterize the animals occupying each burrow system, I attempted to capture all spiny rats resident on the study site during each field sampling period. Animals were captured using 30 × 15 × 15 cm live traps constructed of wire mesh and baited with small slices of squash. Because *T. yonenagae* is nocturnal, traps were set in the afternoon (1600 h) and checked and closed the following morning (0600 h). One to two traps were set simultaneously at all burrow entrances thought to belong to the same system. Trapping of a given burrow system continued until no new animals had been captured at the burrow entrances of that system for 5 consecutive days.

Individuals were considered resident in a given burrow system if they were captured more than twice within the same cluster of burrow entrances during the same field trip. Most (~ 86%) adult males and adult females captured in a given sampling period were resident in the same burrow system throughout the field trip in question (Santos 2004). For the purposes of this study, juveniles were not included in counts of group size due to their obvious association with adult females, but they were used for analyses regarding female fitness.

Animal handling and marking

For all individuals captured, I recorded body weight (using a 300 g Pesola® spring scale), sex, and apparent reproductive status. For females, reproductive condition was determined by visual inspection of the external genitalia (e.g., perforate vagina) and mammae (e.g., enlarged teats characteristic of lactation) and by palpation of the abdomen (for presence of embryos). Because the testes of males of this species never descend and because *T. yonenagae* displays no sexual dimorphism in body size, male reproductive status was determined based on body weight. Specifically, because all reproductively active females weighed ≥ 90 g, I assumed that males weighing ≥ 90 g were also reproductively mature adults (Santos 2004).

Just before their release, newly captured animals were marked with a uniquely numbered metal ear tag (Monel # 1005-1, National Band and Tag Company, Newport, Kentucky) applied to 1 ear. In addition, a small (~ 2 mm square) piece of one ear pinna was removed with sterile surgical scissors and stored in 95% ethanol for subsequent genetic analyses. Each individual was then released into the burrow entrance at which it

had been captured. All animal procedures followed institutional guidelines and the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Measures of social structure

To characterize the structure of groups of conspecifics resident in the same burrow system, the following parameters were quantified:

Group size – the total number of adults resident in a burrow system during a given field sampling period.

Female fitness – the number of offspring produced per female for females resident in the same burrow system during a given sampling period. Per capita direct fitness for females was estimated by determining the total number of juveniles captured in a given burrow system during a single sampling period and dividing this total by the number of adult females resident in the burrow during the same sampling period (Hayes et al. 2009, Lacey 2004).

Adult survival – the proportion of adults captured in the same burrow system during either of the first two field seasons (Feb and Jun 2000) that were recaptured in Jan 2001. Although I could not exclude the possibility that some individuals emigrated from the study area, low rates of adult immigration and evidence of high predation rates during the same period led me to assume that the 'disappearance' of an individual was typically due to mortality (e.g., Ebensperger et al. 2009).

Ecological predictors

To assess the influence of food availability and predator protection on the social structure of the study population, each burrow system trapped during this study was characterized with regard to the following set of variables:

Estimates of food availability – variables used as proxies for food resource availability were distance to *Eugenia* trees (distance to food, or DF) and number of *Eugenia* trees (NET) within a 16 m radius of the geographic center of a burrow system. DF was estimated as the mean of the distance from each burrow opening in a system to the nearest *Eugenia* tree. The radius for estimating NET was based on the mean distance between captures of animals from different burrow systems (15.7 ± 5.4 m, n = 12 pairs of captures) and the maximum distance (14 m) between recaptures of the same individual within a single burrow system. Smaller values for DF and higher values for NET were assumed to indicate greater access to food resources.

Estimates of predator protection – variables used as proxies for predator protection were the number of burrow openings (NBO) per burrow system and the distance to protective vegetation (DPV). DPV was estimated as the mean of the distance from each burrow opening in a system to the nearest macambira. Larger values for NBO were assumed to indicate greater opportunity to escape predators. Smaller values for DPV were assumed to indicate higher degree of protection, since close proximity of burrow openings to protective vegetation should increase an individual's chances of escaping a predator.

Statistical analyses

To avoid violating assumptions of independence underlying my statistical analyses, each burrow system was included in these analyses only once. For burrow systems

trapped during more than one field sampling effort, only data from the first field trip in which the system was monitored were used. Although estimates of adult survival necessarily involved data from more than one field trip, only one estimate per burrow system was included in statistical analyses of this variable.

Data on group size and per capita female reproductive success were not normally distributed and could not be transformed to meet the assumptions of parametric analyses; nonparametric tests were used to examine these variables. Data on adult survival also were not normally distributed. The proportion of adults surviving was arcsin transformed for analysis, although data on survival are presented in the text as untransformed values. I used Kruskal-Wallis ANOVA tests to determine whether group size (number of adults), group composition (number of adults of each sex, number of juveniles), adult survival, and per capita female fitness varied among field sampling efforts. I also used Kruskal-Wallis ANOVAs to determine whether the variables DPV, NBO, DF, and NET were influenced by sampling effort (i.e., season). If these tests were significant, I performed post-hoc Mann–Whitney *U* tests to identify which comparisons yielded significant differences.

To assess the effects of the ecological factors considered on social structure, I used least squares linear regression analyses; because relationships between these ecological variables and social structure had not been examined previously for *T. yonenagae*, I chose to use univariate statistical analyses to explore the effect of each variable individually, rather than as part of a multivariate statistical analysis. Thus, for group size, female per capita direct fitness, and adult survival I tested the predictions that these measures of social structure increased with (1) higher degree of protective vegetation (i.e., a negative association with DPV), (2) greater number of burrow openings (NBO); (3) shorter distances to food (DF), and (4) greater number of *Eugenia* trees (NET) near burrow systems. A variable was considered an important predictor of group size or per capita female fitness if it explained > 10% of the variation in the dependent variables (White 2010) and the associated P value for the predictor was < 0.05.

Statistical analyses were performed using JMP (version 5.0, SAS Institute Inc. 2002). Means are reported ± 1 *SD* with statistical significance set at $\alpha = 0.05$. All statistical tests were 2-tailed unless otherwise noted.

Results

Group composition

A total of 160 adult (68 male, 92 female) and 64 juvenile (31 male, 33 female) *T. yonenagae* were captured during this study. Based on the locations of active burrow entrances, the study site contained a mean of 27.5 ± 8.1 (range = 17-36) occupied burrow systems per sampling period, 13.3 ± 3.9 % (68.7 ± 6.6 %) of which were occupied by groups of ≥ 2 adults (Table 2-1). Since I was interested on variance related to group size and structure, only burrow systems occupied by groups ($n = 53$) were used in the following analyses of ecological influences on social structure.

The total number of adults per burrow system did not differ between seasons (Kruskal-Wallis ANOVA: $H_{3, 53} = 2.42$, $P = 0.077$). Similarly, the number of adult males ($H_{3, 53} = 1.32$, $P = 0.278$), adult females ($H_{3, 53} = 1.69$, $P = 0.182$), and juveniles ($H_{3, 53} =$

2.07, $P = 0.117$) per burrow system did not differ across seasons. When data from all field seasons were pooled, the mean number of adults per burrow system was 2.9 ± 1.3 individuals (range = 2–7, $n = 53$ burrow systems). The mean number of juveniles per burrow system (data from all seasons pooled) was 1.7 ± 0.48 (range = 0-4, $n = 53$ burrow systems).

The total number of adults captured did not differ among field seasons (Kruskal-Wallis ANOVA: $H_{3, 53} = 2.42$, $P = 0.077$). Similarly, neither the total number of adult males ($H_{3, 53} = 1.32$, $P = 0.278$) or females ($H_{3, 53} = 1.69$, $P = 0.182$) captured differed significantly among seasons. The proportion of adults surviving from Feb 2000 to Jan 2000 did not differ significantly from the proportion surviving from Jun 2000 to Jan 2001 (Wilcoxon test: $Z_{1, 21} = 0.08$, $P = 0.851$).

Since capture success was low in Feb 2000 and very few adults from that reduced sample were recaptured in Jan 2001 ($n = 7$ out of 31 adults), captures for the Feb and Jun 2000 sampling periods were combined to allow enough sample size for analyses of survival between the early field seasons and the last one. When data for both time periods were pooled, the proportion of adults surviving did not differ between males and females ($Z_{1, 21} = 0.17$, $P = 0.763$). Using this pooled data set, the mean proportion of males per burrow system surviving until January 2001 was 31.0 ± 24.3 % (range = 0-67 %, $n = 21$ burrow systems). The mean proportion of females per burrow system surviving over the same period was 29.7 ± 27.0 % (range = 0-67 %, $n = 21$ burrow systems).

Since neither sampling interval (Feb-Jan *versus* Jun-Jan) nor sex affected survival, estimates of survival from both intervals and both sexes were pooled to increase the number of individuals and burrow systems included in analyses of survival. Using this pooled data set, mean group size (number of adults per burrow system averaged across all sampling periods during which a burrow system was monitored) did not affect adult survival ($r^2 = 0.08$, $P = 0.217$, $n = 21$ burrow systems), suggesting that greater survival was not simply due to a larger initial number of adults per burrow system.

Food resources

Neither distance to food (DF) (Kruskal-Wallis ANOVA: $H_{3, 53} = 3.17$, $P = 0.060$) nor number of *Eugenia* trees located within a 16 m radius of the center of a burrow system (NET) ($H_{3, 53} = 1.59$, $P = 0.204$) differed significantly between field seasons and thus data for each of these variables were pooled across sampling periods. Using this pooled data set, the mean distance to food was 3.4 ± 2.2 m (range = 0.89-9.41 m, $n = 53$ burrow systems). The mean number of *Eugenia* trees within a 16 m radius was 2.4 ± 1.3 trees (range = 1-6 trees, $n = 53$ burrow systems). When these pooled data sets were examined in relation to social structure, no significant effect of DF was found on group size ($r^2 = 0.03$, $P = 0.228$, $n = 53$ burrow systems), female per capita direct fitness ($r^2 = 0.05$, $P = 0.114$, $n = 53$ burrow systems), or adult survival ($r^2 = 0.00$, $P = 0.997$, $n = 21$ burrow systems) (Figure 2-1). In contrast, number of *Eugenia* trees within a 16 m radius of a burrow system (NET) was significantly positively associated with group size ($r^2 = 0.58$, $P < .0001$, $n = 53$; Figure 2-2a), although NET was not significantly associated with female per capita fitness ($r^2 = 0.00$, $P = 0.667$, $n = 53$; Figure 2-2b) nor adult survival ($r^2 = 0.03$, $P = 0.487$, $n = 21$; Figure 2-2c).

The number of burrow openings per burrow system (NBO) was significantly positively associated with the number of adults resident in a system ($r^2 = 0.21$, $P =$

0.0005, n = 53 burrow systems; Figure 2-3c). At the same time, NBO was significantly negatively associated with distance to food (r^2 = 0.12, P = 0.012, n =53; Figure 2-3a). Combining these outcomes, while distance to food per se did not appear to be an important predictor of social structure, the relationship between group size and number of burrow entrances suggests that members of larger groups did not have to travel as far to access critical food resources.

Predator protection

Neither distance to protective vegetation (DPV) (Kruskal-Wallis ANOVA: $H_{3, 53}$ = 1.65, P = 0.191) nor number of burrow openings per burrow system (NBO) ($H_{3, 53}$ = 2.26, P = 0.093) differed among sampling period. When these data were pooled across seasons, the mean distance to protective vegetation was 1.1 ± 0.7 m (range = 0.1-2.7 m, n = 53 burrow systems) and the mean number of burrow openings per burrow system was 4.0 ± 2.8 openings (range = 1-13 openings, n = 53 burrow systems). Using this pooled data set, DPV was not significantly associated with either female per capita fitness (r^2 = 0.02, P = 0.333, n = 53 burrow systems) or adult survival (r^2 = 0.02, P = 0.504, n = 21 burrow systems), but was significantly positively associated with group size (r^2 = 0.43, P <.0001, n = 53 burrow systems; Figure 2-3b). NBO was significantly positively associated with both group size (r^2 = 0.21, P = 0.0005, n = 53 burrow systems; Figure 2-3c) and female per capita fitness (r^2 = 0.18, P = 0.001, n = 53 burrow systems; Figure 2-3d), but was not significant associated with adult survival (r^2 = 0.07, P = 0.244; n = 21 burrow systems).

Discussion

This study explored the importance of food resources and predator protection as predictors of social structure in *T. yonenagae*. My analyses revealed that while distance to food did not affect any of the measures of social structure considered, the abundance of food resources in close proximity to a burrow system was a significant positive predictor of group size (Table 2-2). With regard to predator protection, the number of burrow openings in a burrow system was a significant positive predictor of both group size and female per capita direct fitness and the distance to protection cover was a significant positive predictor of group size only (Table 2-2). Collectively, these findings indicate that variables related to predator protection were more consistently associated with measures of social structure than were variables related to food resources.

Given that food resources have been identified as important determinants of social structure in multiple mammal species (e.g., Blundell et al. 2002, Brashares and Arcese 2002, Caraco and Wolf 1975) and, more importantly, in several rodent lineages (e.g., Ågren et al.1989, Faulkes et al. 1997, Ostfeld 1986, Slobodchikoff 1984), the absence of stronger effects for distance to *Eugenia* trees or number of *Eugenia* trees in close proximity to burrow entrances is somewhat surprising. It is possible that my measures of food availability did not capture the aspects of this resource that are most closely associated with social structure in *T. yonenagae*. For example, the estimates of space use included in this study (e.g., *Eugenia* within 16 m of the center of a burrow system) were based on capture localities for marked individuals. *T. yonenagae* are nocturnal and

analyses of night time radio fixes currently in progress (Santos, unpubl. data) are revealing that the areas over which members of the study population are active during the night are substantially larger than estimates based on captures, suggesting that my data may substantially underestimate the actual food resources available to residents of a burrow system. The number of *Eugenia* trees within a 16 m radius of the center of a burrow system was significantly associated with group size, suggesting that food resources are important to the study animals; additional analyses that take in to account the full extent and distribution of the resources available to individuals should provide a more accurate picture of the effects of food resources on social structure in *T. yonenagae*.

It is also somewhat surprising that although group size was significantly associated with multiple ecological variables, the other measures of social structure examined were not. Since group size should be determined by the interaction between recruitment of juveniles and loss adults to mortality, it is unclear why group size but not the underlying processes that determine group size should be influenced by environmental variables. Temporal variation in the density of the study population may have created variable opportunities for individuals to disperse to other burrow systems (Lucia et al. 2008, Schradin et al. 2010), but such differences in emigration rates should have been captured in my estimates of adult survival, which did not distinguish between dispersal and mortality. Future studies that examine demographic patterns within the study population in greater detail may help to elucidate how food resources and predator protection impact the processes underlying group size.

Comparisons with other group-living rodents

Predator avoidance has been proposed to favor group-living in other burrow dwelling rodents including degus (Ebnsperger and Wallem 2002), prairie dogs (Hoogland 1981, 1995), and bathyergid mole-rats (Brett 1991, Jarvis and Bennett 1991). In particular, protective vegetation and number of burrow openings have consistently been identified as critical to predator avoidance in semi-fossorial and fossorial rodents (e.g., Cassini and Galante 1992, Hoogland 1981, Tognelli et al. 1995). In degus, access to these forms of predator protection has been shown to be associated with group size (Ebensperger and Wallem 2002). Similarly, among wild guinea pigs (*Cavia aperea*; Cassini and Galante 1992) and southern mountain cavies (*Microcavia australis*; Tognelli et al. 1995), social structure varies with access to protective patches of vegetation. In this study, both distance to protective vegetation and numbers of burrow openings were significantly associated with measures of social structure, suggesting that these forms of predator protection are also important to *T. yonenagae*.

The distribution of critical food resources is also thought to favor group-living in some species of burrow-dwelling rodents, including Mongolian gerbils (*Meriones unguiculatus*; Ågren et al. 1989), California voles (e.g., *Microtus californicus*; Ostfeld 1986), prairie dogs (*Cynomys gunnisoni*; Slobodchikoff 1984, Travis and Slobodchikoff 1993), and bathyergid mole-rats (e.g., *Cryptomys damarensis*; Jarvis et al. 1998). For example, manipulation of food resources to make them more patchily distributed resulted in more extensive overlap of home ranges for female California voles (*M. californicus*; Ostfeld 1986) and increased group size in prairie voles (*M. ochrogaster*; Lin et al. 2006). Similarly, for Gunnison's prairie doges (*C. gunnisoni*), experimental increases in food abundance and patchiness resulted in smaller territories and increased group sizes.

Finally, spatially clumped and unpredictable food resources are thought to favor group-living in Damaraland mole-rats (*C. damarensis*; Jarvis et al. 1998) and other bathyergids (Faulkes et al. 1997, Spinks and Plagányi 1999). In the current study, although number of *Eugenia* trees located in close proximity to a burrow system was significantly associated with group size, a greater number of significant relationships was detected for measures of predator protection suggesting that for *T. yonenagae*, predation is more important than food resources in shaping social structure.

Predator protection and the evolution of burrow sharing in *Trinomys*

The torch tail spiny rat differs from other members of the genus *Trinomys* in that it is burrow dwelling and forms social groups composed of multiple adults (Rocha 1991, Santos and Lacey, in press). In contrast, other members of this genus are forest-dwelling and solitary (Emmons and Feer 1997, Lara and Patton 2000). Although little is known about the behavioral ecology of most *Trinomys*, data from field studies indicate that home ranges of adult female *T. iheringi* do not overlap, which suggests some degree of territoriality in this species (Bergallo 1994, 1995). Experimental encounters conducted in arenas by Freitas et al. (2010) revealed that in contrast to the highly affiliative behaviors recorded for *T. yonenagae*, interactions in *T. albispinus* are generally agonistic, as expected if the latter species is solitary.

It is possible that group-living in *T. yonenagae* has been facilitated by the tendency for this species to live in burrows. Burrows are a crucial microhabitat that allows the animals to escape harsh aboveground temperatures and that offers protection against predators. Since the ancestor of modern echimyids is hypothesized to have been ground dwelling and to have lived in forest habitats (Galewsky et al. 2005), it seems likely that the evolution of burrow dwelling by torch-tail spiny rats was linked to the movement of this species into arid dune habitats. The benefits of occupying burrows (e.g., protection against high temperatures and against predators) may subsequently have favored natal philopatry and group-living in *T. yonenagae*. Comparative studies that contrast the physical conditions and predator pressures experienced by *T. yonenagae* versus other *Trinomys* may help to elucidate the evolutionary series of events that has produced the differences in social structure evident among these animals today.

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Table 2-1. Characterization of groups of *T. yonenagae* resident in 53 burrow systems monitored during 2000-2001. In all cases, all adults resident in the same burrow system during the same field season were captured. Groups consisted of ≥ 2 adults, each of which had been captured at least 2 times in the same burrow system during the same sampling period. Values are presented as average ± *SD*. Data on number of juveniles captured in each burrow system are also shown. Values in parenthesis are ranges.

	Sampling period			
	Feb 2000	Jun 2000	Oct 2000	Jan 2001
Adults per group*	3.9 ± 1.6	3.0 ± 1.1	2.5 ± 0.6	3.1 ± 1.2
	(2 - 7)	(2 - 5)	(2 - 4)	(2 - 6)
Adult females per group*	2.1 ± 1.1	1.9 ± 0.6	1.5 ± 0.6	1.6 ± 0.6
	(0 - 3)	(1 - 3)	(1 - 3)	(1 - 3)
Adult males per group*	1.8 ± 1.2	1.1 ± 0.9	1.0 ± 0.8	1.5 ± 1.2
	(0 - 3)	(0 - 2)	(0 - 2)	(0 - 5)
Juveniles per group*	2.0 ± 1.3	1.3 ± 1.1	0.9 ± 1.0	1.7 ± 1.0
	(0 - 3)	(0 - 4)	(0 - 3)	(1 - 3)
Number of burrow systems	8	13	15	17

Table 2-2. Summary of results of linear regression analyses exploring the effect of 4 ecological variables on measures of social structure. Data are from groups of *T. yonenagae* resident in 53 burrow systems monitored during 2000 to 2001. Ecological predictors were distance to protective vegetation (DPV), number of burrow openings (NBO), distance to food (DF), and number of *Eugenia* trees (NET). A plus (+) sign indicates significant positive association between variables; a minus (-) sign indicates a significant negative association between variables; a zero (0) indicates that no significant association was found between the variables in question.

Measures of social	**Ecological predictors**			
structure	**DPV**	**NBO**	**DF**	**NET**
Group size	-	+	0	+
Female fitness	0	+	0	0
Adult survival	0	0	0	0

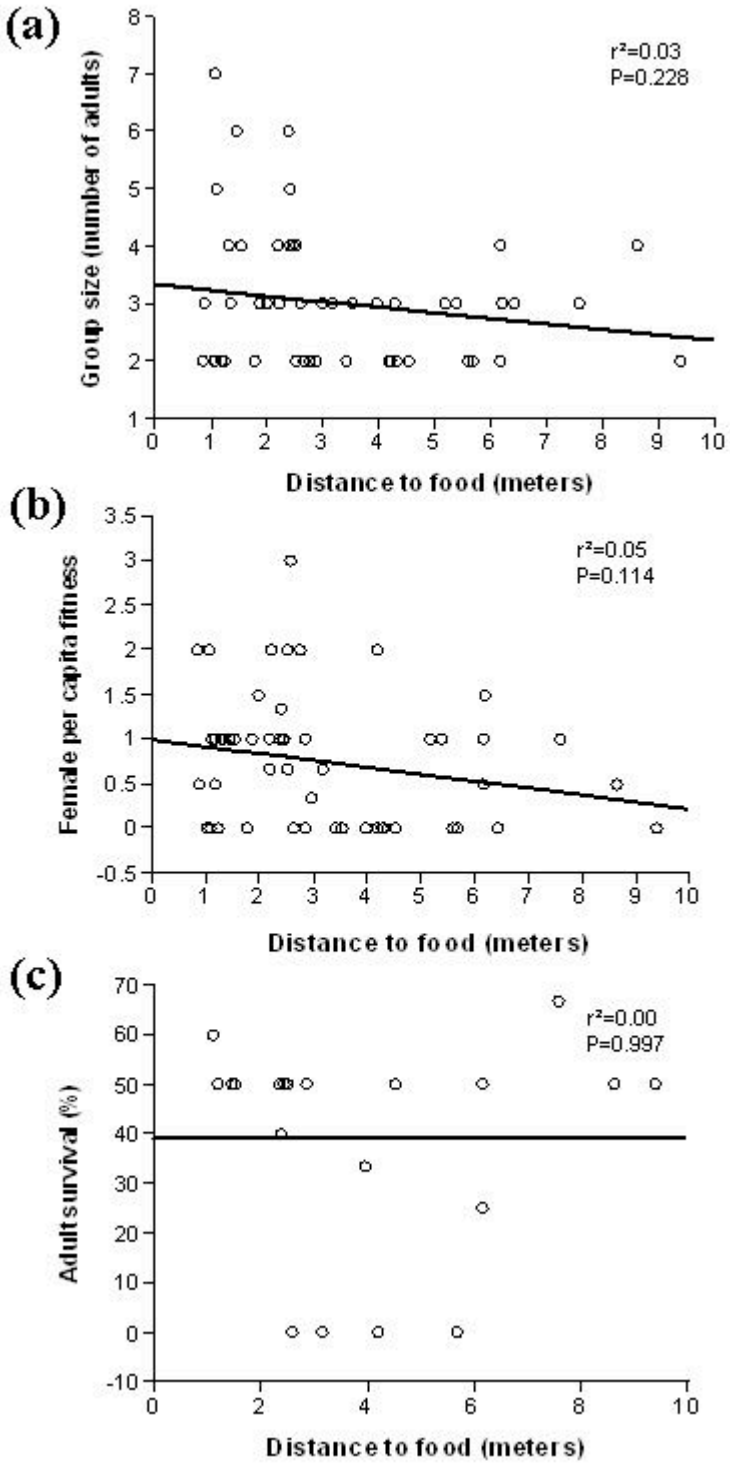

Figure 2-1. Relationships between distance to food and (a) group size, (b) female per capita fitness and (c) percent adult survival. Data are from 53 burrow systems occupied by groups of *T. yonenagae* during 2000-2001. Black lines represent least squares linear regression for the variables analyzed; r-squared (r^2) and P values are provided for each panel.

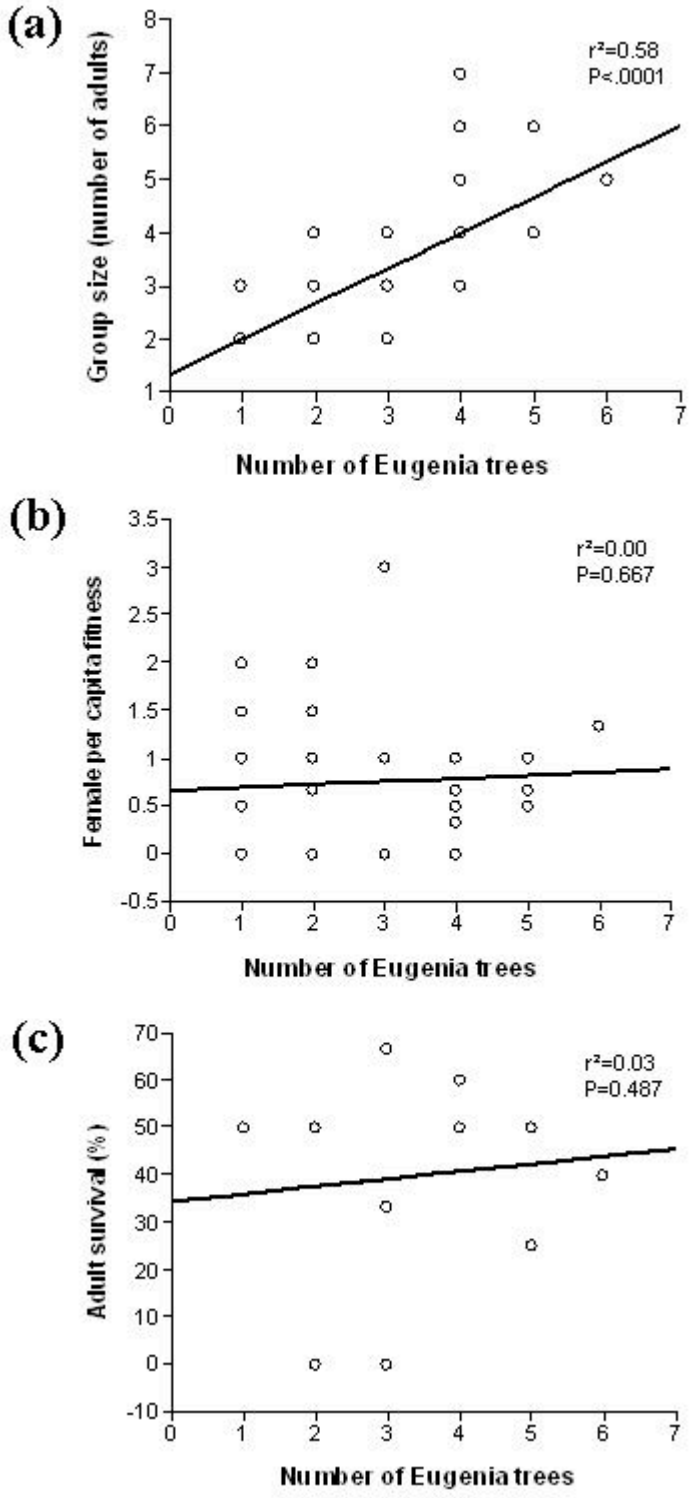

Figure 2-2. Relationships between number of *Eugenia* trees and (a) group size, (b) female per capita fitness, and (c) percent adult survival. Data are from 53 burrow systems occupied by groups of *T. yonenagae* during 2000-2001. Black lines represent least squares linear regression for the variables analyzed; r-squared (r^2) and P values are provided for each panel.

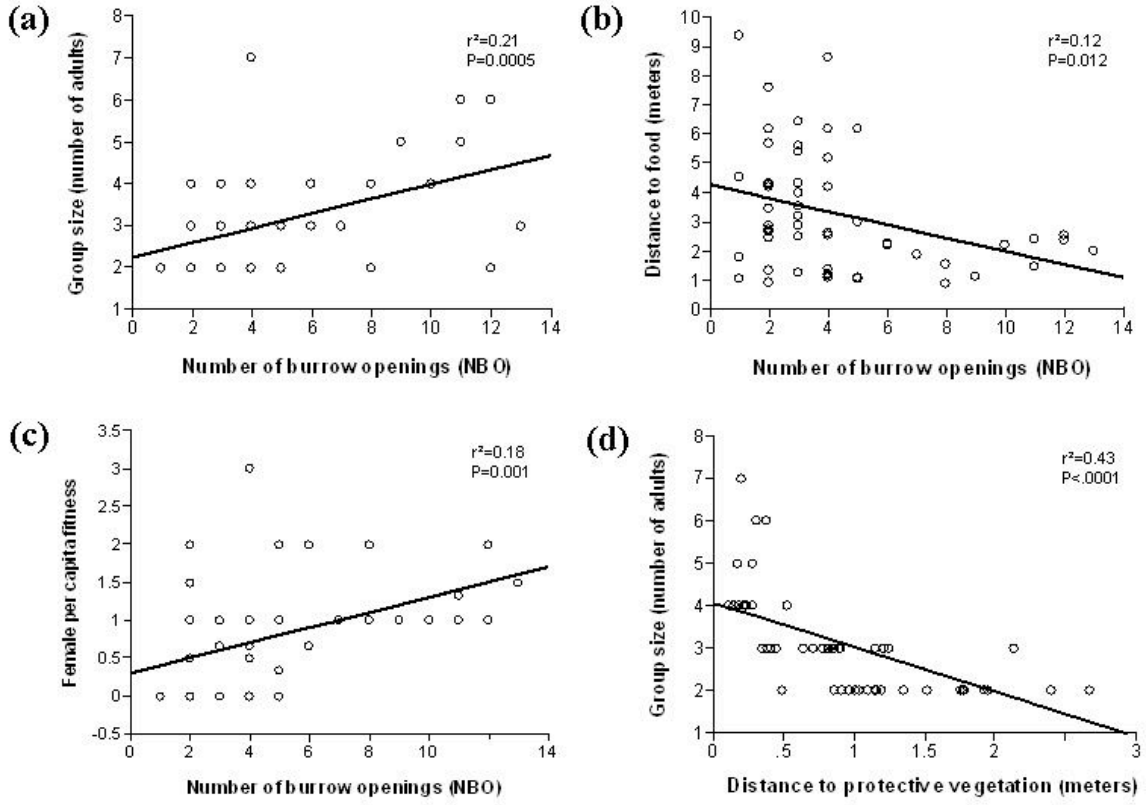

Figure 2-3. Relationships between number of burrow openings and (a) group size, (b) distance to food, and (c) female per capita fitness. Panel (d) depicts the relationship between distance to protective vegetation and group size. Data are from 53 burrow systems occupied by groups of *T. yonenagae* during 2000-2001. Black lines represent least squares linear regression for the variables analyzed; r-squared (r^2) and P values are provided for each panel.

Chapter 3

Kinship and social structure in torch-tail spiny rats, *Trinomys yonenagae* (Echimyidae)

Abstract

Kinship is thought to be an important determinant of individual movement and mate choice, both of which underlie patterns of group structure. Although social groups in many mammal species are composed primarily of closely related females, a growing number of studies indicate that kin structure is complex and varies within groups in ways that are expected to impact individual behavior. As part of ongoing studies of the behavioral ecology of the torch-tail spiny rat (*Trinomys yonenagae*), I combined live-trapping data with analyses of 6 microsatellite loci to characterize the kin structure of this echimyid species, which is distinguished from other *Trinomys* by both its specialization for desert habitats and it tendency to live in groups. My analyses indicate that kinship among adults decreases as the distance between the burrow systems in which they are resident increases. Within burrow systems, relatedness among adult females was significantly greater than that among adult males or male-female pairs. Individuals that dispersed to new burrow systems between field seasons were significantly more related to original opposite-sex burrow mates than were individuals that remained in the same burrow system across years. Relatedness between dispersers and opposite-sex adults was significantly lower in the new (as compared to the original) burrow system. Collectively, these data indicate that social groups of *T. yonenagae* are generally composed of kin, but that dispersal between groups tends to reduce relatedness among group members, in particular opposite-sex adults. These findings are compared to data from other echimyid species to explore how kin structure contributes to reported differences in social structure within this family of Neotropical rodents.

Introduction

Kinship is thought to underlie the nature and dynamics of numerous mammalian social systems (Solomon and French 1997). Formation of kin clusters in these species is regarded to be a critical step in the evolution of complex forms of cooperative interaction, such as altruistic behaviors favored by kin selection (Hamilton 1964, Perrin and Lehmann 2001, West-Eberhard 1975, West et al. 2002; but see Clutton-Brock 2002, 2009, Nowak et al. 2010). For example, in mammals females typically remain philopatric, while dispersal is male-biased (e.g., Croteau et al. 2010, Dobson 1982, Ishibashi and Saitoh 2008, Lacey et al. 1997, Spong and Creel 2001). As a result, groups are expected to consist primarily of female kin (e.g., Armitage 1999, Holekamp and Sherman 1989, Túnez et al. 2009) and cooperative behavior should be most pronounced among females. At the same time, kinship may influence the breeding structure of social groups since closely related individuals may refrain from reproducing with one another (e.g., Armitage 1996, Bengsston 1978, Packer 1985, van Staaden et al. 1994).

While kinship is expected to play an important role in structuring social interactions, accumulating evidence suggests that patterns of dispersal and, hence, kin structure in social mammals are more complex and variable than typically appreciated (e.g., Amos et al. 1993, Blundell et al. 2004, Melnick 1987, Wittemyer et al. 2009). For example, molecular genetic analyses have revealed that although female-biased dispersal is typical of some mammals species (e.g., Munshi-South 2008, Selonen et al. 2010, van Hooft et al. 2008), in others both sexes disperse (e.g., Blundell et al. 2002, Drygala et al. 2010, Fredsted et al. 2007). More generally, social groups may include non kin (Blundell et al. 2004, Hare and Murie 2007, Iacolina et al. 2009, Wolff and Lidicker 1981), indicating that processes other than kin selection (e.g., Clutton-Brock 2002) can favor group formation. As a result, understanding the kin structure of social groups is critical to understanding the fitness benefits available to group members which, in turn, can yield important insights into patterns of cooperation, conflict, and reproduction among group members.

Among echimyid rodents, the torch-tail spiny rat (*Trinomys yonenagae*; Echimyidae) is distinguished by its tendency to live in groups (Chapter 1). While other *Trinomys* are generally forest dwelling and solitary, the torch-tail spiny rat is endemic to semiarid habitat in northeastern Brazil (Rocha 1995), where it inhabits burrow systems in sandy dunes along the left bank of the São Francisco River (Rocha 1995). Previous studies have revealed that *T. yonenagae* exhibits a flexible social structure, with some burrow systems occupied by a single individual and others occupied by groups of 2-5 adults (Santos 2004, Chapter 1). Adults that share a burrow system also tend to share a subterranean nest, where offspring are reared communally (Chapter 1). Field data indicate that while some individuals of both sexes disperse, others are philopatric (Santos 2004), suggesting that kin structure may also vary among groups. To date, however, no studies of kinship within groups of torch-tail spiny rats have been conducted and thus relationships among dispersal patterns, kin structure, and social interactions remain unknown for this species.

The goal of this study is to characterize kin structure in relation to spatial relationships in *T. yonenagae*. In particular, I seek to quantify patterns of relatedness among individuals that share a burrow system. As noted above, field data regarding patterns of dispersal yield conflicting predictions about kinship within groups of *T.*

yonenagae. Provided, however, that at least some individuals are philopatric, burrow mates should on average be more closely related to each other than to animals living in other burrow systems. At the same time, if kinship and inbreeding avoidance are important determinants of the reproductive structure of groups, opposite-sex group mates should be less related than same-sex burrow mates. To test these predictions, I combine spatial data obtained from individually marked torch-tail spiny rats with microsatellite analyses of genetic relatedness in these animals. This is the first characterization of kin structure in the genus *Trinomys*, as well as one of the first (but see Túnez et al. 2009) quantitative analyses of sociality using genetic data in echimyids. These analyses reveal unexpected patterns of relatedness between the sexes that suggest that spacing behavior in this species is influenced by inbreeding avoidance.

Materials and Methods

Study population

This study was conducted on a 5.6 ha area containing 3 parallel sand dunes located along the west bank of the Rio São Francisco, 0.5 km NE of the village of Ibiraba in Bahia State, Brazil (10°47'S, 42°49'W; Figure 1-1). This area was characterized by a semiarid climate with highly seasonal and unpredictable precipitation (annual range = 400–800 mm; Bahia-Seplantec 1978). The rainy season occurred from December to March, with the dry season extending from April to November.

Most (> 75%) of the burrow systems used by torch-tail spiny rats were located on the valley floors between dune summits (Santos 2004). Burrow entrances were typically located under dense clumps of the spiny bromeliad macambira, *Bromelia antiacantha* (Bromeliaceae). Trees in the genus *Eugenia* (Myrtaceae), known as araçá-de-boi, comprised the most abundant woody plant species in the dunes (Rocha et al. 2004); their seeds were the primary food resource consumed by the study animals (Santos 2004).

Burrow systems

Occupied burrow systems were identified by the presence of freshly excavated soil at burrow entrances, footprints of spiny rats in fresh mounds of soil, and remains of recently eaten araçá seeds around burrow entrances (see Chapter 1). All capture locations were recorded by determining the compass direction and distance of the burrow entrance from a fixed, geo-referenced stake placed in the center of each burrow system. I converted each capture locality to x and y values that were plotted on a Cartesian coordinate system, allowing localities for different animals to be mapped relative to one another. Pairwise calculations of the distance between burrow systems were completed using the software package ArcGIS version 9.0 (ESRI Technology Inc., Redlands, California).

Animal capture and handling

To characterize the animals occupying each burrow system, I attempted to capture all members of the study population each year using locally made 30 × 15 × 15 cm live traps constructed of wire mesh and baited with small slices of squash. Because *T. yonenagae* is nocturnal, traps were set in the afternoon (1600 h) and closed the following morning

(0600 h). Trapping was conducted for 10 to 15 days per year, during June to August in 2005 to 2008.

To ensure that only animals using a given burrow system were captured, trap entrances were fitted with a canvas sleeve, the other end of which was attached to a piece of PVC plumbing pipe (see details in Chapter 1). The open end of the PVC tube was placed in an active burrow entrance. As a result, only spiny rats that exited the system via the focal burrow opening could enter the trap, thereby preventing individuals from other systems (i.e., animals traveling above ground) from being captured. Traps were set simultaneously at all burrow entrances thought to belong to the same system, as determined by proximity (Chapter 1) and evidence of recent activity (see above). Individuals were considered residents when captured repeatedly (more than twice) within the same cluster of burrow entrances.

For all individuals captured, I recorded body weight to the nearest gram (300 g Pesola® spring scale), sex, and apparent reproductive status. For females, reproductive condition was determined by visual inspection of the external genitalia (e.g., perforate vagina) and mammae (e.g., enlarged teats characteristic of lactation) and by palpation of the abdomen (for presence of embryos). Because the testes of males of this species never descend and because *T. yonenagae* displays no sexual dimorphism in body size, male reproductive status was determined based on body weight. Specifically, because all reproductively active females weighed ≥ 90 g, I assumed that males weighing ≥ 90 g were also reproductively mature adults (Santos 2004).

To ensure that all animals resident in a burrow system were trapped, each individual captured was placed in a standard polycarbonate rodent cage (dimensions: 40 × 40 × 15 cm), with only individuals trapped in the same cluster of burrow entrances housed in the same cage (≤ 3 adults per cage; see details on Chapter 1). Trapping of a given burrow system continued until no additional animals had been captured, and no activity had been detected at burrow entrances for 48 h (Lacey et al. 1997). Once trapping was complete, all animals held in cages were released at the point of capture.

Just before their release, newly captured animals were lightly anesthetized with isoflurane (Halocarbon Industries, Eagle River, New Jersey), after which they were marked with a uniquely numbered metal ear tag (Monel # 1005-1, National Band and Tag Company, Newport, Kentucky) applied to 1 ear. In addition, a small piece of ear pinna was removed with sterile surgical scissors and stored in 95% ethanol for genetic relatedness analyses. Following recovery from the anesthesia, each individual was released into the burrow entrance at which it had been captured.

All field procedures followed institutional guidelines and the guidelines of the American Society of Mammalogists (Gannon et al. 2007). The study was conducted under permits issued by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA # 0123475 BR, #10959-1).

Spatial relationships and spacing behavior

Trapping records were used to examine the spatial distribution of adult torch-tail spiny rats within and across field seasons. Similarly, trapping data were used to record the presence of juveniles and to document their spatial associations with adults in the study population. Spatial relationships among adults were estimated based on the distance between the geographic centers of the burrow system in which each animal was resident

during a given field season. Individuals were determined to have dispersed if, during successive field seasons, they were resident in distinct burrow systems located > 21 m apart. This distance criterion was based on the mean diameter of individual home ranges (216 ± 88 m^2), as determined from radiotelemetry data collected during the night, when the animals are most active (Santos, unpubl. data); because home range sizes did not differ between males and females (Santos, unpubl. data), the same distance criterion was used for animals of both sexes. In contrast, animals resident in the same burrow system in successive field seasons were classified as not dispersing.

Genetic relatedness

Microsatellite loci

Relatedness among adult torch-tail spiny rats was determined using highly polymorphic microsatellite markers isolated from *T. yonenagae*. A genomic DNA library enriched for microsatellite loci was constructed for *T. yonenagae* following protocols described in Glenn and Schable (2005). In brief, genomic DNA was extracted from ear tissue using a salt extraction protocol developed by Miller et al. (1988). Approximately 2 μg of whole genomic DNA was digested using 10 U *Rsa*1 restriction enzyme (New England Biolabs), after which double-stranded SNX linkers were ligated to both ends of each fragment. Ten microlitres of linker-ligated digest was hybridized to each of following three biotinylated probe mixtures (1 μm): [$(AG)_{12}$, $(TG)_{12}$, $(AAC)_6$, $(AAG)_8$, $(AAT)_{12}$, $(ACT)_{12}$, $(ATC)_8$], [$(AAAC)_6$, $(AAAG)_6$, $(AATC)_6$, $(AATG)_6$, $(ACAG)_6$, $(ACCT)_6$, $(ACTC)_6$, $(ACTG)_6$] and [$(AAAT)_8$, $(AACT)_8$, $(AAGT)_8$, $(ACAT)_8$, $(AGAT)_8$]. Fragments containing microsatellite regions were captured with Streptavidin M-280 Dynabeads (Invitrogen; Life Technologies Corp., Carlsbad, California) and recovered using the polymerase chain reaction (PCR) conditions described in Glenn and Schable (2005).

Microsatellite-enriched PCR products were cloned using a TOPO TA cloning kit (Invitrogen). Sixty three positive (white) clones were amplified using M13 forward with either M13 reverse or T7 primers and sequenced with an ABI 3730 sequencer (Applied Biosystems Inc., Foster City, California). Sequence data were analyzed using the software SEQUENCER version 4.8 (Gene Codes Corp., Ann Arbor, Michigan). Unique microsatellite regions with sufficient (> 50 bp) flanking region sequences were found in 18 clones. Locus-specific PCR primers were designed using the program PRIMER 3 (Rozen and Skaletsky 2000). From those 18 clones, I was able to isolate 12 microsatelite loci. To assess variability at these loci, whole genomic DNA samples from 20 torch-tail spiny rats from twenty burrow systems were amplified with fluorescently labeled primers (6-FAM; IDT, Integrated DNA Technologies, San Diego, California) under optimized PCR conditions (see below). Genotyping was performed on an ABI 3730 sequencer (Applied Biosystems Inc.) using 0.5 μL of PCR product and 0.2 μL of GS500LIZ size standard (Applied Biosystems Inc.) per sequencing well.

PCR and genotyping

All PCR reactions were performed in 10uL volumes in an ABI 2700 thermocycler. Each PCR reaction contained 20 ng of template DNA, 0.2-1.0 μM of each forward and reverse primers, 0.1-0.6 μL 10 mM dNTP, 1.70 μL 10x Roche buffer (Roche Applied Sciences, Penzberg, Germany), 1.2-1.8 μL 25 mM $MgCl_2$, 0.6 μL betaine, and 0.3 μL

Taq polymerase (NEB). Thermal cycling conditions included 95ºC for 3 min, followed by 40 cycles of 94ºC for 30 s, the locus-specific annealing temperature (range = 56-65ºC) for 40 s, and 72ºC for 40 s, with a final extension of 72ºC for 15 min. (Table 3-1). Following amplification, 8 loci consistently yielded clear bands of the expected size range when subjected to gel-electrophoresis on 1% agarose gels stained with ethidium bromide (EtBr). From those eight loci, 6—*Try*1, *Try*3, *Try*5, *Try*7, *Try*11, and *Try*14—were polymorphic (0.95 criterion, Hartl and Clark 1997) and therefore used to genotype individual *T. yonenagae*.

One microlitre of PCR product was then combined with 9.8 µL formamide and 0.2 µL GENESCAN LIZ-500 size standard (Applied Biosystems Inc.) and analyzed on an ABI 3730 sequencer (Applied Biosystems Inc.). All six loci produced consistent, distinct peaks in the resulting electropherograms, whose fragment sizes were analyzed and genotypes assigned by using the software GENEMAPPER version 4.0 (Applied Biosystems Inc.). Raw allele sizes were recorded and then rounded to the nearest integer.

Loci were tested for deviations from Hardy-Weinberg equilibrium (HWE) and genotypic linkage equilibrium using the software GENEPOP version 4.0 on the web (Raymond and Rousset 1995).

Analyses of adult relatedness and parentage

Since null alleles are common in microsatellite data and can bias relatedness estimates (Dakin and Avise 2004), I used the software MICRO-CHECKER version 2.2.3 (van Oosterhout et al. 2004) to verify the presence of null alleles among the set of loci used. I determined the mean pairwise coefficient of relatedness among individuals within the same burrow system and the mean pairwise relatedness of all individuals in the study population using the software ML-RELATE (Kalinowski et al. 2006). This program was selected because it employs a maximum likelihood approach to estimate relatedness and the ML equations used can be modified to account for null alleles, which are considered in all calculations (Kalinowski et al. 2006). Coefficients of relatedness (r) generated by ML-RELATE ranged from 0 (not related) to 1 (highly related).

Statistical analyses

Relatedness data were not normally distributed and could not be transformed to meet the assumptions of parametric tests. Thus, I used a Kruskal-Wallis ANOVA test to assess whether mean relatedness among the adults within a burrow system varied among years. To assess the significance of observed patterns of relatedness among adults in the study population, I compared randomized pairwise r-values, generated by the program RT version 2.1 (Manly 1996), to actual values of r obtained from pairwise comparisons within burrow systems. A Wilcoxon rank sum test (unpaired, non-parametric 2-sample test) was then used to determine whether mean pairwise relatedness among adults within burrow systems differed from random expectations. I used a Kruskal-Wallis test to determine whether mean pairwise relatedness among the adults resident in a burrow system varied among the different types of possible pairs (male-male, female-female, male-female). If appropriate, I then performed LSD post-hoc tests to determine which pairwise comparisons generated significant differences. I used a Wilcoxon rank sum test to determine whether mean pairwise relatedness varied between adults resident in the same burrow system and those resident in different burrow systems.

The relationship between distance (geographic center of the burrow system of residence) and genetic relatedness among adults was examined using least squares linear regression analysis. To determine if changes in the spatial distribution of individuals across field seasons were influenced by kinship, for each individual that dispersed to a new burrow system between field seasons, I calculated the mean relatedness between that animal and the other adults resident in (1) the burrow system left by the dispersing animal and (2) the burrow system joined by the dispersing animal. For animals that remained in the same burrow system in consecutive field seasons, I calculated the mean relatedness between that animal and the other adults resident in the same burrow system in each field season. I then used a Wilcoxon test to compare mean relatedness to adult colony mates for individuals that did and did not disperse between consecutive field seasons; these comparisons were done for all adult burrow mates, as well as for burrow mates of the same and of the opposite-sex. I used a Wilcoxon unpaired test to determine whether dispersal distances varied between males and females. Finally, I used a Fisher's Exact test to compare the proportions of highly related adults (i.e., r-values ≥ 0.25) that remained in the same burrow system in successive years with that of highly related adults that dispersed between field seasons.

Statistical analyses were performed using JMP version 2.0 (SAS Institute Inc., 2002). Means are reported ± 1 *SD* with statistical significance set at $\alpha = 0.05$. Significance levels were adjusted using sequential Bonferroni correction when multiple tests were performed. All statistical tests were 2-tailed unless otherwise noted.

Results

Sample sizes and burrow systems

A total of 246 adult *T. yonenagae* were captured in the study area from 2005 to 2008. Of these, 5 individuals escaped or were killed by predators before they could be individually identified. As a result, 241 individuals were used for analyses of group size, composition and kin structure. Of these, 37 individuals were new captures in 2008 (the last sampling period) and thus could not have been recaptured in a subsequent year; accordingly, a total of 204 individuals (105 males, 99 females) from 44 burrow systems could potentially have been recaptured in successive years. Forty eight (24%) of these animals (24 males, 24 females) were captured during more than 1 field season; these individuals comprised the sample used to examine kinship in relation to the tendency to disperse between field seasons.

Based on the locations of active burrow entrances, the study site contained a mean of 54.8 ± 8.8 (range = 42-60) occupied burrow systems per year. When data from all years were considered, the mean distance between the spatial centers of adjacent burrow systems (as determined from the locations of burrow entrances) was 22.6 ± 7.3 m (range = 8.4-41.7 m, $n = 100$ pairwise comparisons of adjacent systems). No more than one adult per burrow system was recaptured in successive years. Thus, group composition within a given burrow system differed almost completely across years. As a result, I considered data from the same burrow system obtained in different field seasons to be independent for the purposes of examining spatial relationships and genetic relatedness.

Spatial relationships and adult movement

Of the 48 adults captured in successive field seasons, 26 (54%) remained resident in the same burrow system in both years. Sixteen (62%) of these individuals were females and 10 (38%) were males (Table 3-2). The remaining 22 (46%) individuals dispersed to a different burrow system between field seasons. Among those animals that dispersed, 14 (64%) were males and 8 (36%) were females (Table 3-2). For males, the mean distance between the geographic centers of the 2 burrow systems occupied by a dispersing animal was 103 ± 81 m (range = 27-268 m; n = 14 males). For females, this distance was 69 ± 56 m (range = 26-194 m; n = 8 females). Dispersal distances for males and females were not significantly different (Wilcoxon rank sum test: Z = -0.89, P = 0.374). When dispersal distances for the two sexes were pooled, the mean distance between the geographic centers of the 2 burrow systems occupied by each dispersing animal was 91 ± 73 m (range = 26-268 m).

Genetic variation

The number of alleles per microsatellite locus ranged from 9 to 18 (Table 3-1). No evidence of null alleles was detected for any of the 6 loci examined ($P > 0.05$ after Bonferroni correction). Comparisons of observed and expected heterozygosities revealed no significant deviations from Hardy-Weinberg expectations (Table 3-1). No evidence of linkage disequilibrium was detected for the 6 loci examined ($P > 0.05$ after Bonferroni correction).

Kin structure versus spatial relationships among adults

When data from all years were pooled, there was a significant negative relationship ($r^2 = 0.20$, $P < .0001$) between the geographic distance separating the burrow systems in which two animals were resident and their genetic relatedness (Figure 3-1), suggesting that kinship in the study population was spatially structured, with relatedness decreasing as the distance between individuals increased.

Mean pairwise relatedness among adults resident in the same burrow system did not differ across years (2005: 0.21 ± 0.20, n = 58 pairs; 2006: 0.16 ± 0.19, n = 39 pairs; 2007: 0.16 ± 0.22, n = 47 pairs; 2008: 0.22 ± 0.23, n = 35 pairs) (Kruskal-Wallis test: H = 4.53, P = 0.209) and thus I pooled data from all years for subsequent analyses of kinship within versus among burrow systems. Using this pooled dataset, the mean estimated relatedness between randomly selected pairs of adults in the study population was 0.06 ± 0.10 (range = 0.00-0.65, n = 25,621 pairwise comparisons). In contrast, mean pairwise relatedness among adults (both sexes combined) resident within the same burrow system was 0.18 ± 0.21 (range = 0.00-0.65; n = 179 pairs in 54 burrow systems); this difference between observed and randomly generated r-values was significant (Wilcoxon rank sum test: Z = 8.09, $P < 0.0001$). At the same time, mean pairwise relatedness among adults (both sexes pooled) was significantly greater for animals resident within the same (0.18 ± 0.21; n = 179 pairs in 54 burrow systems) versus different burrow systems (0.07 ± 0.11; n = 265 pairs in 62 burrow systems; Wilcoxon rank sum test: Z = 5.37, $P < .0001$). Although adults resident in the same burrow system tended to be more related to one another than to animals resident in other burrow systems, most (74 %) of the burrow systems occupied by groups (n = 16 ± 11 burrows/year) contained ≥ 1 adult that was unrelated to other burrow residents.

Comparisons of mean r-values among adults resident in the same burrow system revealed that females were more related to each other (0.37 ± 0.22, n = 21 pairs in 17 burrow systems) than were males (0.16 ± 0.20, n = 47 pairs in 22 burrow systems) or opposite-sex adults (0.15 ± 0.19, n = 109 pairs in 41 burrow systems); these contrasts were significant (LSD test = 0.12; n = 21, 47, 109; P = 0.001) (Figure 3-2). When each type of dyad was analyzed separately, relatedness for male-male pairs was significantly greater for animals resident within the same burrow system (0.16 ± 0.20, n = 47 pairs in 22 burrow systems) versus animals resident in different burrow systems (0.05 ± 0.09, n = 189 pairs in 32 burrow systems) (Wilcoxon rank sum test: Z = 2.24, P = 0.025). Similarly, relatedness for female-female pairs resident within the same burrow system (0.37 ± 0.22, n = 21 pairs in 17 burrow systems) was significantly greater than that for female-female pairs resident in different burrow systems (0.05 ± 0.08, n = 90 pairs in 37 burrow systems) (Wilcoxon rank sum test: Z = 5.13, P < .0001). Finally, male-female relatedness was significantly greater for animals resident in the same (0.15 ± 0.19, n = 109 pairs in 41 burrow systems) versus different burrow systems (0.06 ± 0.10, n = 450 pairs in 52 burrow systems) (Wilcoxon rank sum test: Z = 4.24, P < .0001) (Table 3-3).

Kinship and adult movements

For animals that were captured in 2 consecutive years, mean pairwise relatedness to burrow mates in year 1 (0.18 ± 0.20, n = 62 pairs in 22 burrow systems) did not differ from mean relatedness to burrow mates in year 2 (0.19 ± 0.21, n = 65 pairs in 19 burrow systems) (Wilcoxon signed rank test: Z = 0.10, P = 0.922). Considering all types of dyads, individuals that remained in the same burrow system across years were not more closely related to their original burrow mates (0.14 ± 0.21, n = 26 pairs in 21 burrow systems) than were individuals that dispersed between years (0.12 ± 0.14, n = 22 pairwise) (Wilcoxon signed rank test: Z = 0.36, P = 0.716). Similarly, individuals that dispersed between years were not more closely related to their original (0.20 ± 0.23, n = 28 pairs in 16 burrow systems) than to their new burrow mates (0.09 ± 0.13, n = 20 pairs in 18 burrow systems) (Z = -0.82, P = 0.412). Thus, overall, the tendency to remain in the same burrow system versus disperse to a new burrow system did not appear to be associated with kinship.

In contrast to these outcomes, which considered average relatedness among all adult dyads in a burrow system, when only relatedness among opposite-sex pairs was considered, however, I found that females that dispersed between years (n = 8) were significantly less related to males in their new burrow system (0.12 ± 0.18, n = 8 pairwise comparisons) than they were to males in their original burrow system (0.32 ± 0.16, n = 8 pairwise comparisons) (Wilcoxon signed rank test: Z = 2.07, P = 0.038). Similarly, males that dispersed between years (n = 14) were significantly less related to females in their new burrow system (0.08 ± 0.11, n = 14 pairwise comparisons) than to females in their original burrow system (0.27 ± 0.17, n = 15 pairwise comparisons) (Wilcoxon signed rank test: Z = 3.11, P = 0.002) (Table 3-4). These results suggest that animals of both sexes reduced relatedness to burrow mates by dispersing to new burrows.

To explore this pattern in greater detail, I examined relatedness among opposite-sex pairs for individuals that remained in the same burrow system in consecutive years. Mean pairwise relatedness between adults captured in successive years and their opposite-sex burrow mates in year 1 did not differ between males (0.09 ± 0.11, n = 11 pairwise

comparisons) or females (0.07 ± 0.11, n = 16 pairwise comparisons) (Wilcoxon rank sum test: $Z = 0.36$, $P = 0.716$) and thus I pooled data for philopatric males and females. Using this pooled dataset, the mean pairwise relatedness between individuals that remained in the same burrow system in successive years and their opposite-sex burrow mates in year 1 (0.08 ± 0.11, n = 16 pairwise) was significantly less than the relatedness between individuals that dispersed between field seasons and their opposite-sex burrow mates in year 1 (0.29 ± 0.17, n = 22 pairwise) (Wilcoxon rank sum test: $Z = 4.43$, $P < .0001$). For adults that remained in the same burrow system in successive years, only 3 (11%) out of 27 pairwise comparisons with adult burrow mates revealed r-values ≥ 0.25, versus 13 (59%) of 22 such comparisons for adults that dispersed between field seasons; these proportions were significantly different (Fisher's Exact test: $\chi^2 = 13.30$, $d.f. = 1$, $P = 0.001$). Collectively, these data suggest that kinship among opposite-sex adult burrow mates may be an important determinant of the tendency to disperse to a new burrow system. Moreover, these findings regarding individual movement, burrow occupancy, and kin structure suggest that social units (i.e., the animals resident within a burrow system) do not consist exclusively of close kin groups, but instead include immigrants from other burrow systems.

Discussion

This study examined how genetic relatedness among individual *T. yonenagae* co-varied with the spatial distribution and movements of adults. Overall, genetic kinship declined with the distance between the burrow systems in which individuals were resident. Accordingly, kinship among adults resident in the same burrow system was greater than that among adults resident in different burrow systems; this tendency was evident for male-male and mixed-sex pairs and was most pronounced for female-female pairs. Adults of both sexes were captured in successive field seasons, with roughly half of these individuals dispersing to a new burrow system between seasons. For both sexes, adults that dispersed between seasons were more related to opposite-sex adults in their original burrow than in their new burrow. In general, individuals that remained in the same burrow system in successive years were less related to opposite-sex burrow mates than were adults that dispersed between field seasons. Thus, kinship appeared to be associated with the movement patterns of individuals within the study population.

One potential bias in these findings is the temporal scale over which data were collected. Torch-tail spiny rats can reach adulthood within 6 months of birth (Santos, unpubl. data), with the result that my annual sampling regime may have failed to capture some members of the study population. At the same time, predation pressure on the study animals is believed to be intense (Santos 2004, Chapter 2), a suggestion that is supported by the high turnover of adults between years reported here. Although under-reporting of dispersal or similar events is likely, there is no reason to expect that this would have systematically biased the analyses of kinship reported here. Thus, while future studies of these animals would benefit from employing a more frequent sampling regime, the data reported here should provide a robust picture of relationships between spatial distribution and kinship in the study population.

Kin structure in torch-tail spiny rats.

Within burrow systems, adult *T. yonenagae* were generally related to both same and opposite-sex individuals. This finding is consistent with the prediction that *T. yonenagae* social units consist of family groups. The formation of stable kin groups is generally thought to be a prerequisite for kin selection (Alexander et al. 1991, Chesser 1991), which can influence the evolution of social behaviors (Alexander 1974). Moreover, the finding that females are most related suggests that kin-selected behaviors may be more common in this sex and may help to explain anecdotal observations of allolactation among female burrow mates (Sena and Santos, unpubl. data). At the same time, however, the presence of unrelated individuals within most groups of *T. yonenagae* suggests that selective forces other than kin selection may play a role in shaping social behavior in this species (e.g., Clutton-Brock 2002, 2009). The prevalence of groups composed of both related and unrelated adults may be reflected in the highly affiliative behaviors observed among *T. yonenagae* captured in different burrow systems (Freitas et al. 2003, Freitas et al. 2010). In sum, group structure in *T. yonenagae* is likely influenced by kin selection, although the nature and magnitude of indirect fitness benefits likely varies among group mates.

Kinship and patterns of movement

Dispersal is a fundamental phenomenon that underlies the demographics, genetics, and behavior of a population (Lidicker and Stenseth 1992). Therefore, characterizing patterns of individual movement is crucial to understanding patterns of group formation and structure. Dispersers of both sexes were significantly more related to original burrow mates of the opposite-sex than to opposite-sex adults in the burrow system to which they moved. One interpretation of these data is that individuals disperse to decrease their relatedness to potential mates (Wolff and Lidicker 1981). Inbreeding avoidance is thought to play an important role in the demography of many species (Ralls et al. 1986) and one commonly proposed mechanism of inbreeding avoidance is sex-biased dispersal (Cockburn et al. 1985, Koenig et al. 1996, Pusey and Packer 1987). Interestingly, however, my analyses indicated that *T. yonenagae* of both sexes disperse; although this tendency is more pronounced among males, dispersal is not as sex-biased as in other group-living rodents (e.g., *Cynomys ludovicianus*, Dobson et al. 1997; *Microtus arvalis*, Gauffre et al. 2009; *Rhombomys opimus*, Randal et al. 2005; *Ctenomys sociabilis*, Lacey et al. 1997). Future studies that track the movements of known individuals throughout their lifetimes and that use genetic data to quantify patterns of reproductive success within groups should help to elucidate the relationship between dispersal, kinship, and inbreeding avoidance in *T. yonenagae*.

As noted above, dispersal in several other species of social, burrow dwelling rodents is strongly male-biased. Perhaps not surprisingly, for these species, relatedness among female group mates is high, with adult males typically being much less related (or even unrelated) to the females with which they live (Cutrera et al. 2005, Dobson et al. 1997, Ishibashi and Saitoh 2008). Different patterns of dispersal and kin structure, however, have been reported for other species of burrow-dwelling rodents. For example, in talar tuco-tucos (*Ctenomys talarum*), although extirpation studies have revealed that juveniles of both sexes disperse (Malizia et al. 1995), genetic analyses revealed that only females resident in neighboring burrow system were close kin (Cutrera et al. 2005). In contrast,

studies of banner-tailed kangaroo rats (*Dipodomys spectabilis*) have revealed that, in this species, both males and females are philopatric (Jones et al. 1988) and, accordingly, both sexes exhibit genetic kin structure as a function of distance from their natal burrow (Winters and Waser 2003). Interestingly, these animals appear to avoid inbreeding by traveling away from the area in which they are resident when seeking mates (Winters and Waser 2003). Clearly, burrow-dwelling species differ with regard to patterns of individual movement, providing opportunities for comparative studies aimed at identifying relationships among dispersal, kinship, and social structure.

Comparisons with other echimyids

Studies on social behavior in spiny rats (family Echimyidae) are rare and most of their social systems are basically unknown (Lacher 1982). Although some studies have suggested that many echimyids are solitary (e.g., *Trinomys iheringi*, Bergallo 1995; *Thrichomys apereoides*, Streilein 1982; *Proechimys guairae*, Aguilera 1999; *Proechimys cuvieri*, Guilliotin 1982; *Proechimys brevicauda*, Emmons 1982), others have revealed that social structure in these animals may be more complex. For example, in island populations in Gatun Lake, Panama, adult Tome's spiny rats (*Proechimys semispinosus)* were found to commonly co-occupy burrows (Endries and Adler 2005). In southern Brazil, juvenile southern bamboo rats (*Kannabateomys amblyonyx*) appear to delay dispersal, leading to the formation of family groups (Silva et al. 2008). Kin structure in these species, however, has not been examined using genetic markers. Indeed, the only other echimyid for which molecular markers have been used to assess relatedness is the semi-aquatic coypu (*Myocastor coypus*), which lives in groups composed of related adult females and one or more unrelated adult males (Túnez et al. 2009). Thus, while few studies of genetic relatedness in echimyids have been completed, the available data suggest that kin structure varies among members of this family, including among species characterized by some degree of group-living. As additional studies of social and kin structure in echimyids are completed, a more comprehensive comparative picture of sociality in these hystricognath rodents should emerge.

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Table 3-1. Characteristics of 6 microsatellite loci isolated from *T. yonenagae* including 5′–3′ primer sequence, annealing temperature (ºC), PCR product size (bp), and number of alleles. T_a is the annealing temperature used in PCR reactions.

Locus	Primer sequences (5′–3′)	T_a (ºC)	PCR product size (bp)	No. of alleles	H_o	H_e	Hardy-Weinberg *P* value
*Try*1	F: FAM-CAGGCCTCTGTTGGTCTGTT R: TGCAGACTGAGCTCTACAAGG	60	108-126	9	0.900	0.876	0.867
*Try*3	F: FAM-TGACCTTGAAGACACCAGGA R: TCTGATGACAATGAACCCGTTA	63	115-137	9	0.800	0.776	0.130
*Try*5	F: FAM-TGACCACATGAGGCTTTTGA R: CCCAACAGGATAGAGGACAGA	65	201-255	18	0.900	0.932	0.510
*Try*7	F: FAM-GCAGAATCACAGCACTTCCTT R: TGTTTTTCCTGGCCTTTCAT	56	253-275	9	0.850	0.873	0.336
*Try*11	F: FAM-TACAAGCGCAAGCTGCATAC R: TCAATCTGCAAAACTTCCCTTA	61	162-208	11	0.850	0.899	0.066
*Try*14	F: FAM-GGGGGAGGAGAGAAATTGAG R: ACCAGGAGTGCCAGATTTTG	56	90-124	13	0.900	0.905	0.496

Table 3-2. Inter-year movements in male and female *T. yonenagae* regarding their burrows of residence during 2005 to 2008.

Sex	Total	Spacing behavior	
		No dispersal	Dispersal
male	24	10 (38%)	14 (64%)
female	24	16 (62%)	8 (36%)
total	48	26 (54%)	22 (46%)

Table 3-3. Average relatedness in sex pairs (male-male, female-female, male-female) of *T. yonenagae* within and between burrow systems during 2005 to 2008. Values in parenthesis are number of pairwise. Asterisks indicate statistically significant comparisons.

Sex pairs	Relatedness **within** burrow systems	Relatedness **between** burrow systems	*P* value
male-male	0.11 ± 0.15 (*n* = 47)	0.05 ± 0.09 (*n* = 189)	0.025*
female-female	0.39 ± 0.22 (*n* = 21)	0.05 ± 0.08 (*n* = 90)	<.0001*
male-female	0.17 ± 0.20 (*n* = 109)	0.06 ± 0.10 (*n* = 450)	<.0001*

Table 3-4. Average relatedness among *T. yonenagae* that dispersed and their opposite-sex mate(s) within original burrow systems as compared to average relatedness among dispersers and adults within burrow systems to which they dispersed. Values in parenthesis are number of pairwise. Asterisks indicate statistically significant comparisons.

Disperser sex	Relatedness among opposite-sex adult(s) **within original** burrow system	Relatedness among opposite-sex adult(s) **within new** burrow system	*P* value
male	0.27 ± 0.17 (*n* = 15)	0.08 ± 0.11 (*n* = 14)	0.002*
female	0.32 ± 0.16 (*n* = 8)	0.12 ± 0.18 (*n* = 8)	0.038*

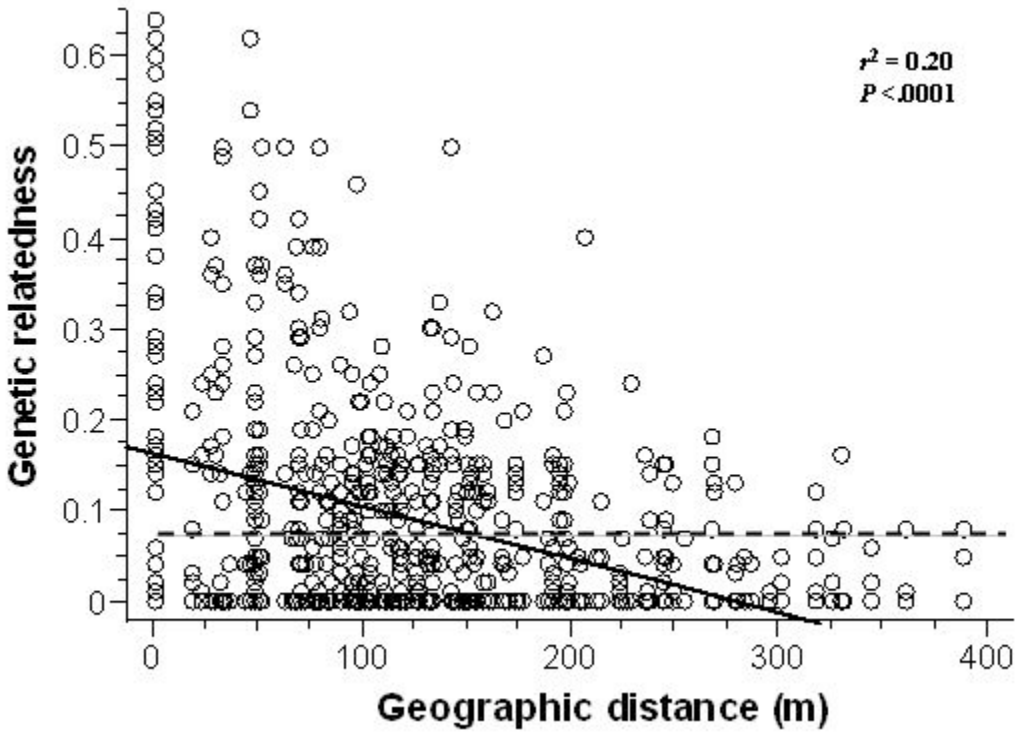

Figure 3-1.Relationship between geographic distance (meters) and genetic relatedness in a population of *T. yonenagae*. Data are from 1059 pairwise comparisons during 2005 to 2008. Black line represents least squares linear regression and dashed line represents grand mean; r-squared (r^2) and P values are provided.

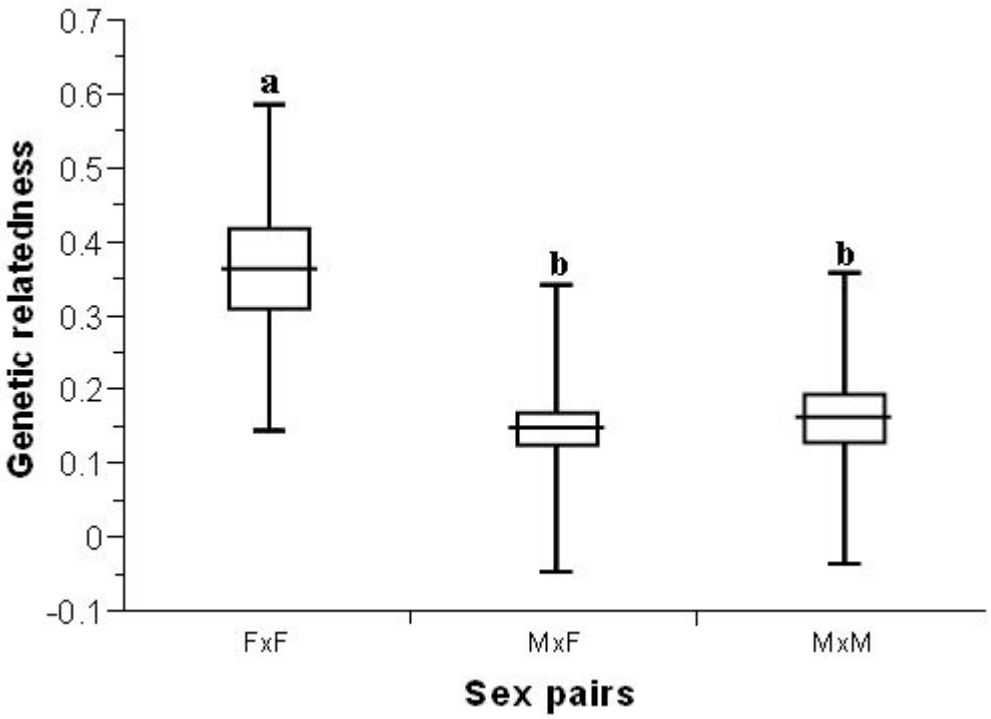

Figure 3-2. Comparisons of estimated relatedness between adult *T. yonenagae* sex pairs within burrow systems (FxF = female × female, MxF = male × female, MxM = male × male) during 2005 to 2008. Values are presented as average ± *SD*. Different letters indicate statistically significant differences.

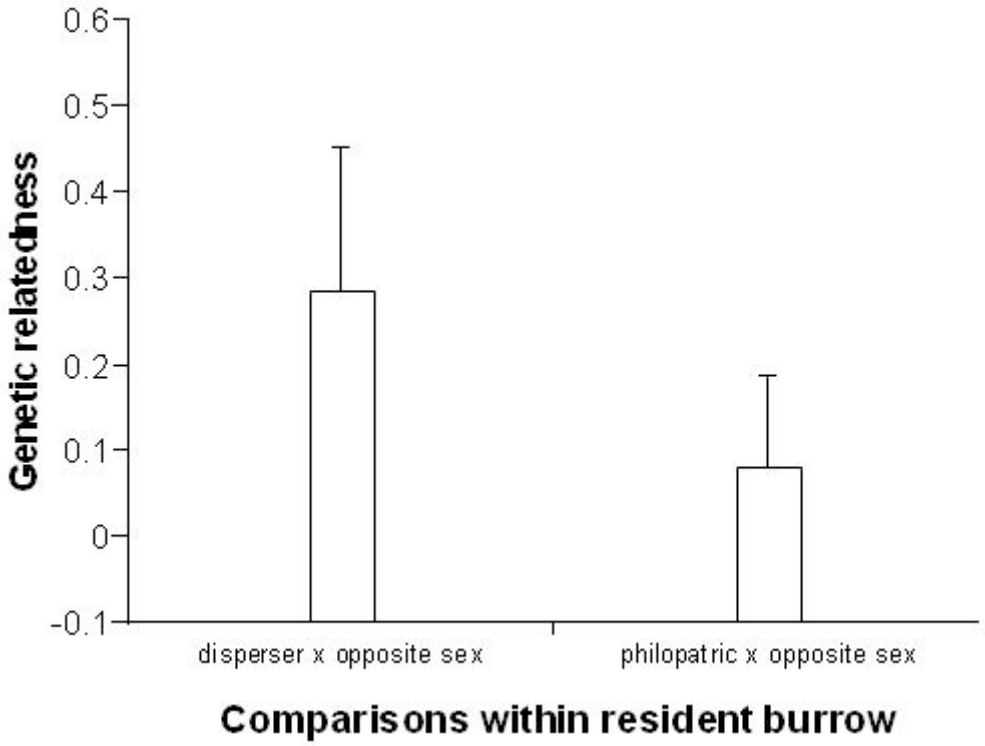

Figure 3-3. Comparison of average relatedness among dispersing and philopatric *T. yonenagae* and former opposite-sex mates within resident burrows systems from 2005 to 2008. Values are presented as average ± *SD*.

Chapter 4

Epilogue

Evolution of sociality in torch-tail spiny rats

In this dissertation, I examined multiple aspects of the social structure and the ecology of the group-living in torch-tail spiny rat, *Trinomys yonenagae*. Although this Neotropical rodent is endemic to semiarid dune habitats in northeastern Brazil, it is part of a genus composed primarily of solitary, forest-dwelling species. The invasion of this environment by *T. yonenagae* was likely correlated with the divergences in morphology, ecology, and behavior that distinguish this species from other members of the genus *Trinomys* (Rocha 1995). At the same time, these traits reflect convergence with other desert rodents (Mares 1980). Although *T. yonenagae* is not as specialized for desert habitats as some other rodent lineages (e.g., kangaroo rats, genus *Dipodomys*), my study animals exhibit a number of locomotor, sensory, and behavioral adaptations typically associated with such habitats (Mares 1980).

Interestingly, water balance in *T. yonenagae* is not significantly different from that in other species of *Trinomys* (Mendes et al. 1998); rather than physiological adaptations (e.g., kidney function) to cope with water stress, it is possible that some of the distinctive behavioral attributes of *T. yonenagae* (e.g., burrow dwelling) are adaptive responses to selective pressures imposed by an arid environment. Support for this hypothesis comes from Rocha (1991), who demonstrated that *T. yonenagae*, like other echimyids, are extremely susceptible to high temperatures and dry air, such as occur aboveground in the dune habitat occupied by these animals. Based on these findings, Rocha (1991) proposed that burrow-dwelling by *T. yonenagae* is part of a set of crucial evolutionary changes that made it possible for these animals to invade arid habitats.

Once burrow-dwelling had become established in this species, the high energetic costs of constructing or expanding burrow systems may have favored group-living as a means of energy conservation (Ebensperger and Bozinovic 2000). Anecdotal observations both from the field and the lab suggest that torch-tail spiny rats cooperate to dig burrows. Santos (2004) hypothesized that group-living could serve to reduce the energetic costs to individuals living in such microhabitats. The outcomes of the present study support this hypothesis and suggest that burrow systems not only provide protection from harsh extrinsic conditions, but also function as an important form of protection against predators. Thus, group-living and cooperative burrow excavation may be essential components of the ability of *T. yonenagae* to endure in a harsh, open environment.

Directions for future research

My analyses of the ecological correlates of sociality in *T. yonenagae* revealed that protection provided by spiny vegetation is a good predictor of group size in this species. Future field studies that experimentally manipulate the vegetation cover associated with individual burrow systems could be used to directly test the importance of this resource in

group formation, size, and persistence. Similarly, the reported correlation between proximity of food resources and group size could be tested experimentally. Specifically, adding *Eugenia* fruits near occupied burrow systems should lead to increases in the sizes of the social groups inhabiting those systems. Because the magnitude of this effect may vary seasonally, ideally this manipulation should be repeated in both the wet and dry seasons that characterize the study area and extended over multiple years.

My studies of relatedness and individual movements in torch-tail spiny rats revealed intriguing patterns of burrow occupancy, social structure, and dispersal. Social groups in the study population were generally composed of close kin, although unrelated adults were also detected within groups. These findings support previous hypothesis that selective forces other than kin selection have contributed to shaping the social behavior of this species (Freitas et al. 2010). Overall, *T. yonenagae* appears to possess most of the behavioral attributes associated with cooperative breeding in vertebrates (*sensu* Alexander et al. 1991), namely: (i) reduced territoriality and high affiliation among group members; (ii) sharing of a burrow system by multiple adults, including a common nest; (iii) pronounced care of young; and (iv) overlap of generations, presumably as a result of natal philopatry. Future studies that explore social interactions among group members in greater detail should help to determine the extent to which burrow mates cooperate with one another, including participating in alloparental care of young.

Conclusions

This study represents one of the first detailed analyses of the behavioral ecology of an echimyid rodent. In addition to increasing our knowledge of this important family of rodents, the analyses presented here add to our understanding of several critical aspects of rodent social behavior, including the ecological correlates of sociality, the relationships among group-living, space use, and demography, as well as the role of kinship in influencing the structure and dynamics of their societies. Thus, studies of *T. yonenagae* represent an important addition to the growing comparative picture of the ecology of sociality in rodents.

Perhaps more importantly, these findings have crucial implications for policies regarding the conservation of *T. yonenagae* and the sustainable use of the dune habitats in which this species occurs. Currently, these habitats are becoming fragmented due to human driven activities (e.g., grazing of livestock, wood extraction, uncontrolled fires). The data presented here can be used to evaluate how habitat fragmentation may impact the social structure and demography of torch-tail spiny rats. For example, my analyses indicate that torch-tail spiny rats do not use space homogeneously. Instead, individuals concentrate residence and activity primarily on the valleys, where their burrow systems are better protected by spiny vegetation. Analyses of dispersal events also indicate that most dispersers move to burrow systems in the same valley where their original systems were located. Thus, the plateaus separating these valleys presumably function as semi-porous barriers that contribute to enhance genetic differences between populations of different valleys. Occasionally, a few dispersers cross these plateaus and such dispersal events are thought to contribute for inbreeding avoidance. Given that dispersal may be an important mechanism of inbreeding avoidance, loss of habitat caused by the ongoing impacts may lead to local extinction of *T. yonenagae* populations and, therefore, increase inbreeding among members of the remaining occupied burrow systems. Collectively,

these data imply that adequate conservation measures should consider the heterogeneity of these dune habitats as much as other measures taken into account, such as the size of the area to be preserved. Specifically, target preservation areas regarding torch-tail spiny rats should harbor as many valleys as possible, which would ensure proper space use and facilitate adequate levels of genetic diversity.

Because *T. yonenagae* is considered a keystone species (e.g., seed disperser, shelter provider for other vertebrates, main prey item for wildlife species) the maintenance of populations of this species has significant implications for the conservation of other elements of biodiversity found in the São Francisco River dunes. Thus, the data presented here are crucial not only to understanding the natural history of a threatened species (Catzeflis et al. 2008), but also to providing a foundation for sound conservation decisions regarding a recently recognized biological hotspot (Rodrigues 2003, Tabarelli and Silva 2003).

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