

ACTIVITY PATTERNS IN TWO RODENT COMMUNITIES
AT EL CIELO BIOSPHERE RESERVE,
TAMAULIPAS, MEXICO

A Senior Honors Thesis

By

ANGELA D. SKEELES

Submitted to the Office of Honors Programs
& Academic Scholarships
Texas A&M University
in partial fulfillment of the requirements of the

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RESEARCH FELLOWS

April 2003

Group: Education, Business, and Life Science

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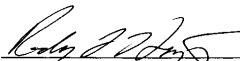
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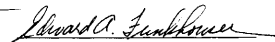
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ABSTRACT

Activity Patterns in Two Rodent Communities at El Cielo Biosphere Reserve,
Tamaulipas, Mexico

(May 2003)

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Today, natural systems are undergoing drastic human-induced changes and losses of biodiversity. During this time of change it is extremely important that we understand the underlying mechanisms controlling the structure and composition of biotic communities. Small mammal communities have been studied extensively in arid regions (Brown et al. 2000), but few studies have been conducted in tropical regions. In 1957 Hutchinson proposed niche division as a means of co-existence of similar species. In 1974 Schoener proposed that the dietary, spatial, and temporal were the three main axes along which niche division may occur. This study evaluated the temporal patterns of the rodent communities at two sites in El Cielo Biosphere Reserve, Tamaulipas, Mexico. The first site was located in the Tropical Sub-Deciduous Forest (TSDF) region of the reserve. Six rodent species were trapped during interval trapping: *Liomys irroratus* (Heteromyidae), *Peromyscus levipes* (Muridae), *Peromyscus leucopus* (Muridae), *Baiomys taylori* (Muridae), *Sigmodon hispidus* (Muridae), and *Oryzomys couesi* (Muridae). All species at both sites are nocturnal and granivorous. We used chi-

square and G-test analyses and rejected our null hypothesis (Time periods during the night were utilized equally) for all species except for *P. leucopus*, which had an extremely small sample size. We constructed a null model using Gotelli's Ecosim program against which to test Pianka's niche overlap index, and found that $p(\text{observed} \leq \text{expected}) = 0.91$ (Gotelli and Entsminger 2001). Likewise, at the second site, located in the Cloud Forest (CF) region, we rejected our null hypothesis for both species (*P. levipes* and *P. ochraventer* (Muridae)). $P(\text{observed} \leq \text{expected}) = 0.87$. We concluded that there is a very small chance the patterns observed in either site are random, and thus there is likely an underlying mechanism shaping these patterns. We also observed that *O. couesi* and *L. irroratus* overlapped in their spatial and dietary niches, but were separated by their temporal niche utilization. The temporal niche aspect is rarely included in the many studies focusing on dietary and spatial niches. There are still many aspects of activity patterns that are poorly understood.

DEDICATION

I dedicate this thesis to my parents, Martha and James Skeeles, and Thomas E. Lacher, Jr. My parents have dedicated themselves to my and my sisters' success and happiness. For 21 years they have and continue to be an unending source of support and love. Dr. Lacher has given me the guidance, confidence and encouragement to pursue my dreams. He is an incredible mentor, teacher, and friend.

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Introduction

As a result of explosive human population growth and development, our natural landscapes are undergoing massive global alterations. Now more than ever it is important to understand the underlying processes structuring ecosystems and biological communities. The perturbation of natural communities by human activities has prompted many authors to suggest that our planet is experiencing inflated rates of extinction (Chapin et al. 2000; Myers and Knoll 2001). Therefore, understanding the organization of natural communities and ecosystems is of utmost importance, especially for the decipherment of processes responsible for the maintenance of biodiversity in natural ecosystems (Janzen, 1997). Through such knowledge, one may be able to mitigate against human activities that disrupt the natural organization of communities and ecosystems.

One of the key questions in community ecology relates to how species that utilize similar resources can co-exist within a community (Brown et al. 2000). Since the early 1990s, there has been considerable debate regarding the rules governing community structure and composition (Clements, 1916; Gleason, 1926). In 1975 Diamond coined the term assembly rules, referring to patterns of co-existence, and ever since community ecologists have debated processes responsible for the assembly of natural communities (Stone et al. 2000).

This thesis follows the style and format of the *Journal of Mammalogy*.

Since Hutchinson's landmark paper in 1957, niche separation has been considered a major contributor to the co-existence of species. Schoener (1974), while recognizing the complexity of niches occupied by multiple taxa, identified the partitioning of resources (e.g., habitat, food, and time) as the major means of accommodating multiple species with niche overlap. Of these three, he considered time to be the least important, as 78% of the cases examined appeared to involve niche partitioning in response to food. However, Shoener (1974) did note that under severe predation pressure the temporal axis would likely be a more crucial factor. Subsequent to Shoener's proposals, few studies have addressed situations of temporal niche partitioning, especially in relation to diet and habitat (Halle and Stenseth 2000).

Park (1940) and others (Brown 1956; Bruseo and Barry 1995; Glass and Slade 1980; Kolter et al. 1993; Miller 1955; Mitchell et al. 1990; O'Farrell 1974; Pearson 1962; Wojcik and Wolk 1985; Ziv et al. 1993) have recognized the ecological and evolutionary significance of activity patterns, yet few have focused on the integration of all three niche dimensions including time, area, and resources, especially in habitats with a complex community structure (Castro-Arellano, personal communication). In such complex communities, niche partitioning may be extremely crucial (Pianka 1974; Wilson 1999).

Temporally, organisms synchronize their internal clock according to tide cycles, light and dark cycles, the lunar cycle, and seasons (Aschoff 1984). Circadian clocks, however, are generally thought to be synchronized with the light-dark (LD) cycle (Bartness and Albers 2000). These general patterns in association with the LD cycle can

be described as nocturnal, diurnal, or crepuscular (Brown 1956). However, there are many exceptions in small mammals, one being shrews and voles, species that are active during both day and night and display polyphasic or acyclic activity patterns (Baumgardner et al. 1980; Crowcroft 1953; Daan and Slopsema 1978; Halle 1993; Halle 2000b; Hamilton 1937). This is commonly attributed to unique metabolic demands (Baumgardner et al. 1980; Daan and Slopsema 1978; Ruf and Heldmaier 2000). Circadian rhythms have been observed in laboratory conditions in the absence of light, and are considered internal (Aschoff 1984; Hamilton 1937; Stephan 1981).

Activity patterns also can be influenced by environmental factors such as moisture, light, and temperature, all of which vary significantly according to time of day (Halle 2000a). These factors, along with activity patterns, demonstrate seasonal variation (Mueller and Mueller 1979; Lockhard and Owings 1974; Miller 1955). In addition, biotic factors such as interspecific competition (Crowcroft 1953; Glass and Slade 1980; O'Farrell 1974; Pianka 1974), social factors (Bartness and Albers 2000), opportunity for foraging (Drickamer and Springer 1998; Kenagy 1973; Kolter et al. 1993; Ziv and Smallwood 2000), predation pressure (Belovsky et al. 1989; Caraco 1980; Daan and Slopsema 1978; Daly et al. 1992; Gerell 1969; Gerkema and Verhulst 1990; Halle 1993; Kalcelnik and Bateson 1996; Lima 1998; Lima and Dill 1989; Peterson and Batzli 1975; Smallwood 1996), and parasitic/pathenogenic pressure can affect activity patterns (Halle and Stenseth 2000). Too few studies of activity patterns under either field or laboratory conditions have been initiated to test these factors.

Empirical studies have focused on either circadian rhythms or activity budgets (Lima and Dill 1990; Kacelnik and Bateson 1996; Smallwood 1996), and are primarily laboratory based (Baumgardner et al. 1980; Boulos et al. 1979; Dewsbury 1980; Kavanau 1969; Stephan 1981). Lab work in these areas is crucial to our understanding of the mechanism of activity rhythms. Nevertheless, if one is to understand the complex ecological and evolutionary processes associated with the development of activity patterns, field experiments that consider both abiotic and biotic factors must be conducted (Ashby 1972; DeCoursey 1990; Enright 1970; Halle and Stenseth 2000; Park 1940). Furthermore, the number of studies in more tropical regions is minimal, yet community structure can be highly complex (Castro-Arellano personal communication; Wilson 1999). The objectives in this study are to provide a detailed assessment of niche overlap and activity patterns in a rodent guild located in Neotropical regions of northern Mexico. In this guild several species of rodents presumably display considerable niche overlap, especially with respect to food preferences. Therefore, my hypothesis is that species with the most habitat and/or food resource overlap should display less overlap in terms of 24h activity patterns.

Methods and Materials

Description of Study Area and Rodent Community

The El Cielo Biosphere Reserve is located in southwest Tamaulipas Mexico, about 320 miles from the Texas border. The area of 144,530 hectares was designated a reserve in 1985 (Valiente-Banuet et al. 1995; Vargas-Contreras and Hernandez-Huerta

2001). The reserve is located in the Sierra Madre Oriental Mountain range, and has altitudes ranging from 200 to 2300 m above sea level. Environmental parameters vary along the altitudinal gradient that crosses four distinct vegetation zones, Tropical Subdeciduous Forest, Cloud Forest, Pine-Oak Forest and Xerophitic Scrub. Faunal elements in this region are unique, being characterized by high rates of endemism and biodiversity. In addition, small mammal composition includes species from both the Nearctic and Neotropical biogeographic regions, with more tropical species reaching their northern-most distribution in this area (Hershkovitz 1958). Although El Cielo is a reserve, the region still experiences impact from human land-use practices. For instance, the eastern side of the reserve is dominated by agricultural use (Castro-Arellano, personal communication), and considerable alterations have occurred since the last inventory of mammalian species in the region (as reviewed in Vargas-Contreras and Hernandez-Huerta 2001).

Censusing of Small Mammals

Time-interval surveys were conducted at two sites. The first was located at Los Cedros Biological Station in Gomez Farias (23°02'58N, 099°09'06W) in the Tropical Sub-deciduous forest vegetation type (TSDF). This site was the lowest in elevation at about 300 meters. Temperatures generally ranged from 36-39°C during the summer months. Typical vegetation included *Bursera simaruba*, *Lysiloma divaricata*, *Savia sessiliflora*, *Drypetes latelifolora*, *Brosium alicastrum* and *Achatocarpus nigricans* (Valiente-Banuet et al., 1995). The second site was located in the Cloud Forest (CF), near the town of San Jose. Here vegetation composition varied considerably, with the

dominant species being *Liquidambar styraciflua*, *Quercus sartorii*, *Quercus germana*, and *Clethra pringlei* (Puig et al., 1983). Also, the understory was much less dense. Temperatures were quite a bit lower, ranging generally from 17-19°C.

At both sites, trap transects consisting of Sherman live traps were used to estimate both abundance and activity patterns, especially as they relate to the use of microhabitats. Trap surveys at both sites were conducted from June-August in 2001 and in May to August in 2002. Traps nights at the TSDf and CF sites were 3,650 total trap and 860, respectively. Since all trapping occurred during the summer, no evaluation of seasonal differences in activity pattern could be assessed. Furthermore, it has been firmly established that many prey and predator species alter their behavior according to the lunar cycle (Daly et al. 1992; Lockard and Owings 1974; O'Farrell 1974). For this reason, I conducted activity trapping only during new moon phases. Trapping is the oldest and possibly most frequently utilized method in activity pattern studies (Brown 1956; Drickamer and Springer 1998; Hamilton 1937; Miller 1955; O'Farrell 1975; Peterson and Batzli 1975). Other methods such as radio-telemetry and automatic recording have also frequently been employed (Daly et al. 1992; Matsubayashi et al. 2003). However, Halle and Stenseth (2000) weighed the disadvantages and advantages of all three methods and found trapping to be the best overall method. We used 8 by 9 by 23 cm Sherman live traps arrayed in transects of 160-180 traps. The traps were divided into two transects set in different locations within each vegetation type, and the stations were set approximately 7 meters apart. Traps were checked every 2h period, as this has been established as a standard time interval for activity studies (Brown et al.

1956; Daan and Slopsema 1978; Drickamer and Springer 1998; O'Farrell 1974). Stenseth and Halle (2000) suggest using an attractive bait. I used a mixture of peanut butter, oats, and vanilla. When an animal was caught it was removed from the transect and replaced with another baited trap. Captured animals were taken back to camp and processed the next day. It was found that releasing the animals causes a bias due to a higher probability of re-trapping the animal (Castro-Arellano, personal observation). Although all species are known to be highly nocturnal or crepuscular, traps were left open during the day to register any diurnal activity. No diurnal activity was registered. Daylight spanned from about 700h to 2030h. Each night traps were set by 1900h and checked every 2h period until 700 hours.

Statistical Analyses

A Chi-Square test was used to determine whether each species was using the 2h periods equally. The null hypothesis was that the species were dividing activity equally among the 2h intervals throughout the night. However, according to Williams (1967) the Chi-Square test is not always accurate, especially in cases of exceptionally small sample size. In such cases he suggested the use of a Log-Likelihood Ratio, or a G-test. I used this test for species with low sample size, such as *Oryzomys couesi* (n=11) and *Baiomys taylori* (n=12). However, for comparative purposes I conducted both Chi-Square and Log-Likelihood ratio tests for all species. Values were not calculated for *Peromyscus leucopus* due to extremely small sample size (n=3). Additionally, simple body mass ratios were calculated between species to compare body size. (Table 3). This also provides a rough idea as to which species have similar metabolic requirements.

It is assumed in community ecology that interspecific competition reduces niche overlap (Gotelli and Entsminger 2001a). Therefore, if interspecific competition is occurring in a community, one should observe less niche overlap than expected by chance. Null models provide a simulation of results produced randomly to test against experimental results. Originally, there was a considerable amount of debate surrounding the use of these models, but they have become both improved and widely used (Gotelli 2001). Current controversy is focused mainly on mathematical details of null models (Gotelli and Entsminger 2001b). In 1967 MacArthur and Levins proposed the first index of niche overlap. Feinsinger et al. (1981) noted that even in the absence of competition niche division still occurs. Therefore, it is important to compare experimental results against situations that might occur randomly in nature. I used Gotelli's Ecosim program to create a null model against which to compare observed estimates of Pianka's niche overlap and Czechanowski's index values (Gotelli and Entsminger, 2001a). I used the default conditions for number of iterations (1000), niche breadth (retained), zero states (reshuffled), and resource states (equiprobable) (Gotelli and Entsminger 2001a). These default conditions produce a RA3 randomization algorithm (Gotelli and Entsminger 2001a) that Winemiller and Pianka (1990) found to have good statistical properties for detecting non-random niche overlap patterns.



FIG. 1. Location of El Cielo Biosphere Reserve

Results

Small mammals captured at site one represented two families and six species including: *Limomys irroratus* (Heteromyidae), *Peromyscus leucopus* (Muridae), *Peromyscus levipes* (Muridae), *Baiomys taylori* (Muridae), *Sigmodon hispidus* (Muridae), and *Oryzomys couesi* (Muridae). All members of Muridae are also classified in the subfamily Sigmodontinae. *L. irroratus*, or the Mexican spiny pocket mouse, is a medium-sized grey mouse with sharp, hispid pelage. It occurs in Mexico and extreme southern Texas. In Northern Mexico it occurs in dense chaparral and along stone fences and along rocks. It has external fur-lined cheek pouches. It is granivorous and strictly nocturnal (Davis and Schmidly 1994). *Peromyscus leucopus*, or the white-footed mouse, is a medium-sized, with a short tail and sharply bicolor pelage. It generally lives in woodland habitats, except in the western part of their range. It is a granivore species, but also feeds on nuts such as acorns and pecans (Davis and Schmidly 1994). They are nocturnal (Bruseo and Barry 1995; Dewsbury 1980). *Peromyscus pectoralis*, or the white-ankled, mouse is very similar in appearance to *Peromyscus leucopus*, but has a much longer tail in relation to the rest of its body. It is a rock-dwelling species and a granivore (Davis and Schmidly 1994). *Oryzomys couesi* is a medium sized rat with tawny colored pelage that is usually associated with water (Davis and Schmidly 1994). *Baiomys taylori*, or the northern pygmy mouse, is by far the smallest of the rodents captured at the reserve. It resides in the tropical lowlands of Mexico, and meets its upper range limit in Texas. These mice prefer open or grassy areas, and along railroads and highway right-of-ways are often found in association with *Sigmodon hispidus* (Davis and

Schmidly 1994). *Sigmodon hispidus*, or the hispid cotton rat, is a moderately-large rat with black-grey hispid pelage. It prefers grassy areas with good cover. They mainly feed on plant material, but are also known to feed on the eggs of ground-nesting birds (Davis and Schmidly 1994).

Two species, *Peromyscus ochraventer* and *Peromyscus levipes*, were captured at site two (CF). Both are members of Family Muridae and subfamily Sigmodontinae.

Peromyscus ochraventer is endemic to the area.

Based on chi-square and log-likelihood values the null hypothesis was rejected for all six species found at TSDF site (Tables 1 and 2). Therefore, none of these species were dividing their time equally throughout the night. Although the chi-square test rejected the null hypothesis for *Oryzomys couesi* (n=11) and *Baiomys taylori* (n=12), the test is not always valid in analysis of small sample sizes (Williams 1976) (Table 1). Therefore, for these two species I relied more on the Log-Likelihood or G-test (Zar 1996), which also rejected the null hypothesis (Table 2).

Using Gotelli's Ecosim program to construct a null model to test against observed calculations of Pianka's index of niche overlap revealed significant deviation of observed from expected ($p = 0.79$) for the TSDF community, suggesting less niche overlap than expected from the null model. For the CF community the p value was 0.87, again suggesting less niche overlap than predicted under the null model. Using Czechanowshi niche overlap index and a null model, the TSDF revealed a p value of 0.91 and CF community 0.89. I also used Ecosim to calculate Pianka's niche pairwise overlap index values (Table 3). These values represent the degree of niche overlap

between species pairs (0=no resource overlap; 1=complete resource overlap) (Gotelli and Entsminger 2001a). In the CF community the pairwise index value was calculated as 0.91.

Finally, I determined the peaks of activity for each species (except for *Peromyscus leucopus* (n=3) due to small sample size). *Liomys irroratus* clearly reached its peak activity in the latter part of the night (Fig. 2a). *Sigmodon hispidus* exhibited a strongly crepuscular activity pattern (Fig. 2b), and *Peromyscus levipes* in the TSDF had a sharp increase in activity following sunset, but appeared active throughout the night without a distinctive peak (Fig. 2c). *Oryzomys couesi* exhibited a bimodal pattern occurring early in the night (Fig 3a). In fact, *Oryzomys couesi* is the only species besides *Peromyscus leucopus* that did not exhibit activity in the 5AM-7AM period (Fig. 2; Fig. 3). Finally, *Baiomys taylori* exhibited a peak at the beginning of the night, and a slighter peak at the end (Fig. 3b). At the CF site both *P. levipes* and *P. ochraventer* had peaks of activity in the early part of the night, and activity declined in the latter part of the night (Fig. 4). *P. levipes* had a similar activity pattern at both the CF and TSDF sites, but with a stronger early peak of activity at the CF site (Fig. 5).

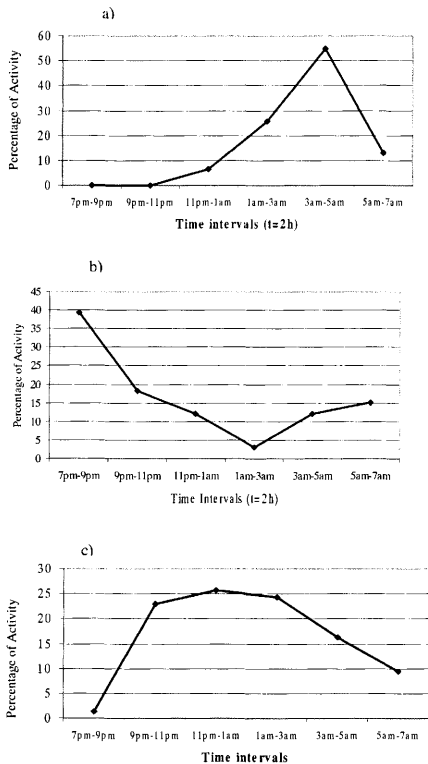


FIG. 2. – Percentage of activity at the TSDF site by 2h time period for a) *Liomys irroratus* b) *Sigmodon hispidus* and c) *Peromyscus levipes*

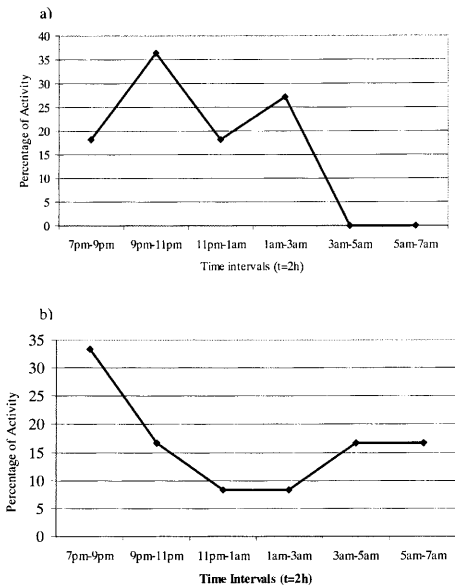


Fig. 3. – Percentage of activity at the TSDF site by 2h time period for a) *Oryzomys couesi* b) *Baiomys taylori*

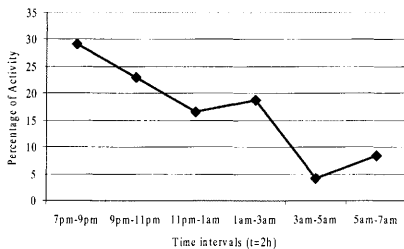
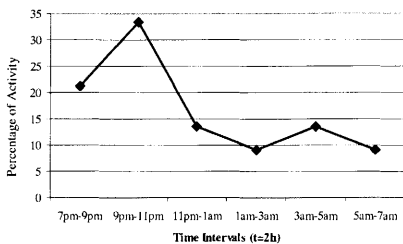


FIG. 4. —Percentage of activity at CF site by 2h time period for
a) *Peromyscus levipes* b) *Peromyscus ochraverter*

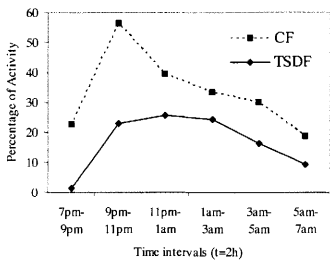


FIG. 5.—Comparison of Activity Patterns of *Peromyscus levipus* in Cloud Forest and Tropical Sub-deciduous forest

TABLE 1.—Chi-Square Values

Species	Site	Chi-Square	Reject Null Hypothesis
<i>Peromyscus levipes</i> (n=74)	TSDf	20.70	Yes
<i>Liomys irroratus</i> (n=31)	TSDf	41.17	Yes
<i>Sigmodon hispidus</i> (n=33)	TSDf	14.82	Yes
<i>Oryzomys couesi</i> (n=11)	TSDf	7.01	No
<i>Baiomys taylori</i> (n=12)	TSDf	3.00	No
<i>Peromyscus levipes</i> (n=66)	CF	17.09	Yes
<i>Peromyscus ochraventer</i> n=48)	CF	12.25	Yes

df=5 ¹Significant at $\alpha=0.05$; ² $\alpha=0.025$; ³ $\alpha=0.01$; ⁴ $\alpha=0.005$; ⁵ $\alpha=0.001$

TABLE 2.—Log-likelihood (G-Test) values

Species	Site	Log-Likelihood Ratio	Reject Null Hypothesis
<i>Peromyscus levipes</i> (n=74)	TSDf	27.33	Yes
<i>Liomys irroratus</i> (n=31)	TSDf	41.65	Yes
<i>Sigmodon hispidus</i> (n=33)	TSDf	13.95	Yes
<i>Oryzomys couesi</i> (n=11)	TSDf	49.31	Yes
<i>Baiomys taylori</i> (n=12)	TSDf	45.77	Yes
<i>Peromyscus levipes</i> (n=66)	CF	15.48	Yes
<i>Peromyscus ochraventer</i> n=48)	CF	13.7	Yes

df=5 ¹Significant at $\alpha=0.05$; ² $\alpha=0.025$; ³ $\alpha=0.01$; ⁴ $\alpha=0.005$; ⁵ $\alpha=0.001$

TABLE 3. Pianka's Niche overlap index pairwise comparisons in the TSDF community. (0=no resources in common; 1=complete overlap)

	<u><i>L. irroratus</i></u>	<u><i>S. hispidus</i></u>	<u><i>O. couesi</i></u>	<u><i>B. taylori</i></u>	<u><i>P. leucopus</i></u>
<i>Peromyscus levipes</i>	0.627	0.527	0.825	0.603	0.719
<i>Liomys irroratus</i>		0.332	0.252	0.492	0.093
<i>Sigmodon hispidus</i>			0.655	0.979	0.386
<i>Oryzomys couesi</i>				0.667	0.623
<i>Baiomys taylori</i>					0.327
<u><i>Peromyscus leucopus</i></u>					

Discussion

Based on the results from all tests, one can conclude that the observed activity patterns of rodents in communities at both TSDf and CF sites are not a result of random occurrences. However, the more difficult question relates to the underlying mechanisms responsible for these non-random patterns. Competition is assumed to be the primary mechanism of assembly rules (Brown et al. 2000), yet it cannot be directly verified by testing. Nevertheless, one can assume that competition is active to when less niche overlap is observed than expected values from a null model (Gotelli and Entsminger 2001a). One also would expect to observe more competition in a species-rich community, such as seen at the TSDf site (Pianka 1974; Wilson 1999).

The temporal and spatial niches are closely related and should be studied together (Halle 2000a; Holling 1992). All species in this study are granivores (seed-eating), and therefore have similar diets. In 2000-2001 Castro-Arellano conducted a study examining the microhabitat use of the rodents found at TSDf and CF sites at El Cielo (unpublished data). He constructed Cluster analyses showing the similarity of habitat usage of the species in the community (Fig. 6-7). At the CF Site *P. levipes* and *P. ochraventer* were observed to use highly similar microhabitats, yet were still strongly divided by slope and distance to rocky outcrops (Fig. 6) (Castro-Arellano personal communication). Although included in the analysis, the other species did not have large enough sample sizes to be discussed. At the TSDf site there are two distinct groups of similar microhabitat use. *B. taylori*, *L. irroratus*, *O. couesi*, and *S. hispidus* comprise one, while species of *Peromyscus* comprise the other.

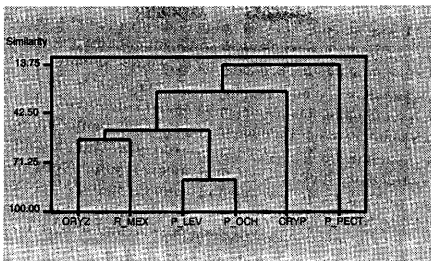


FIG. 6. Cluster Analysis of Microhabitat use at the CF Site. *Oryzomys couesi* (ORYZ), *Reithrodontomys mexicanus* (R_MEX), *Peromyscus levipes* (P_LEV), *Peromyscus ochraventer* (P_OCH), (CRYP), and *Peromyscus pectoralis* (P_PECT). From Castro-Arellano unpublished data

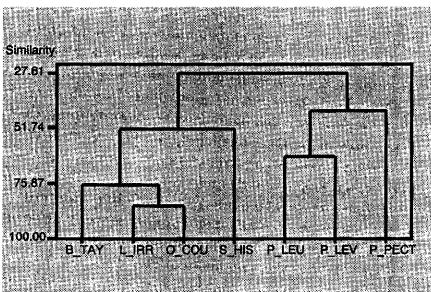


FIG. 7. Cluster Analysis of Microhabitat use at the TSDF Site. *Baiomys taylori* (B_TAY), *Liomys irroratus* (L_IRR), *Oryzomys couesi* (O_COU), *Sigmodon hispidus* (S_HIS), *Peromyscus leucopus* (P_LEU), *Peromyscus levipes* (P_LEV), *Peromyscus pectoralis* (P_PECT). From Castro-Arellano unpublished data

Also, *L. irroratus* and *O. couesi* have particularly similar microhabitat uses. *B. taylori* is also closely related to these species, yet sample sizes were small. Body size is an extremely important factor to consider. As small endotherms with high surface-area to volume ratios, rodents have high metabolic constraints (Halle and Stenseth 2000). Species of similar sizes are more likely to be in direct competition. The calculated body mass ratios between species provide a rough idea of similarity of metabolic requirements (Table 4).

TABLE 4. Body mass ratios of species found at both TSDF and CF Sites

Species	R MEX	P LEU	P PEC	P LEV	P OCH	L IRR	O COU	S HIS
B_TAY	1.59	2.07	2.57	2.72	3.60	3.90	4.20	7.81
R_MEX	XXX	1.30	1.61	1.71	2.26	2.45	2.64	4.90
P_LEU		XXX	1.24	1.31	1.74	1.88	2.03	3.77
P_PEC			XXX	1.06	1.40	1.52	1.63	3.04
P_LEV				XXX	1.32	1.44	1.55	2.87
P_OCH					XXX	1.08	1.17	2.17
L_IRR						XXX	1.08	2.00
O_COU							XXX	1.86

P. pectoralis (P_PEC), *P. levipes* (P_LEV), *P. ochraverter* (P_OCH), *Liomys irroratus* (L_IRR)
Oryzomys couesi (O_COU)

I observed a very interesting relationship between *Oryzomys couesi* and *Liomys irroratus* at the TSDF Site. First, *Oryzomys couesi* has a very strong peak of activity during the earlier part of the night (7pm-3am) (Fig. 3a). In contrast, *Liomys irroratus* peaks in activity during the latter part of the night (11pm-7am) (Fig. 2a). The rest of the species, although peaking at different times, tend to be active throughout the night (Fig.

2-3). Pianka's pairwise niche overlap index value (0.252) supports this apparent temporal niche separation between the two species (Table 3). This value is the lowest for all pairs of species, except *Liomys irroratus* and *Peromyscus leucopus*. However, it should be noted that *P. leucopus* has a sample size of only 3 individuals. In contrast, *L. irroratus* and *O. couesi* have very similar microhabitat usage (Fig. 6). They are also similar in body size, with a body mass ratio of 1.08 (Table 4). For two species so similar in microhabitat use and body size, separation along the niche axis seems to be important for their co-existence.

One can postulate that this separation is due to competition, yet it could be simply a circumstance of other factors, such as predation avoidance or exposure. Many authors feel that the beginning of night is optimal for foraging and provides other advantages related to sexual interactions and exposure to optimal temperatures (Kenagy 1973; Kolter et al. 1993; Ziv and Smallwood 2000). However, Drickamer and Springer (1998) found subordinate *Mus domesticus* males to forage at the beginning of the night while dominant males forage during the latter part of the night. There is not enough information to make an inference regarding the subordination or dominance of either species in the current study.

Several unanswered questions remain. First, sample size is an issue and limits effective evaluation of relationships between *P. leucopus* and *B. taylori* relative to other elements of the community as well as to each other. Larger sample sizes of *O. couesi* are necessary for determining its relationship to *L. irroratus*. Laboratory experiments and experimental removal of individuals of a species would further help one understand

the activity patterns observed in this study. Second, seasonal variation in activity patterns has been observed in small mammals and generally reveals pronounced trends (Mueller and Mueller 1979; Lockhard and Owings 1974; Miller 1955). It would be particularly interesting to conduct censusing over other seasons. Third, moonlight avoidance, or decreased activity in accordance with increased moon illumination and thus increased predation risk, has been observed in many situations (Daly et al. 1992; Lockard and Owings 1974; O'Farrell 1974). It would be interesting to conduct this study during different phases of the moon to observe how individual species respond to environmental cycles. Fourth, in a few cases, reproductive states of animals have been found to influence activity patterns (Bruseo and Barry 1995). Also, Drickamer and Springer (1998) observed juveniles and adults to have differential activity patterns. They attributed this to the high surface area to volume ratio of juveniles and decreasing temperatures in the latter part of the night. In my study, there was preliminary evidence for juveniles being active during different times from adults. However, sample sizes are too small to derive any significant inference from these observations. Finally, the dynamics of predator/prey activity patterns has been widely studied (Belovsky et al. 1989; Caraco 1980; Daan and Slopsema 1978; Daly et al. 1992; Gerell 1969; Gerkema and Verhulst 1990; Halle 1993; Kalcelnik and Bateson 1996; Lima 1998; Lima and Dill 1989; Peterson and Batzli 1975; Smallwood 1996) but parasitic and pathenogenic effects on activity patterns are poorly understood (Halle and Stenseth 2000).

The niche concept provides a formal characterization of how selection in an environment can result in changes in components of a community through adaptation.

Enright (1970) stated that “it is self-evident to most ecologists that the time domain is an important aspect of adaptation.” Despite this statement, empirical evidence for such a time dimension is lacking (Brown 1956; Bruseo and Barry 1995; Glass and Slade 1980; Kolter et al. 1993; Miller 1955; Mitchell et al. 1990; O’Farrell 1974; Pearson 1962; Wojcik and Wolk 1985; Ziv et al. 1993). The preliminary results presented in this paper suggest that there is a temporal dimension to the partitioning of niches for species of rodents with similar food preferences, and the overall community structure of rodents deviates from that expected on the basis of null models. Therefore, these data are compelling in that they suggest avoidance of competition by temporal partitioning of the niche. Clearly, these data must be considered preliminary, as they are limited in sample size and seasonal coverage. Hopefully, these parameters can be explored further in the near future.

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