Journal of Tropical Ecology (2012) **28**:65–72. © Cambridge University Press 2011
doi:10.1017/S0266467411000551

Co-occurrence of small mammals in a tropical dry deciduous forest: comparisons of communities and individual species in Colima, Mexico

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(*Accepted 23 September 2011*)

Abstract: Species co-occurrence is an important ecological research area. Mark-and-recapture studies of mammals allow identification of coexisting species, a necessary step in determining mechanisms enabling habitat sharing. Using data from five 1-ha grids in January 2004 in tropical dry deciduous forest of coastal Colima, Mexico, we detected significantly more interspecific overlap than expected between seven species pairs. *Oryzomys couesi* shared more stations than expected with *Sigmodon mascotensis*, *Baiomys musculus* and *Peromyscus perfulvus*. *Baiomys musculus* was associated positively with *S. mascotensis* and *Reithrodontomys fulvescens*. *Heteromys pictus* shared fewer stations than expected with *O. couesi* and *S. mascotensis*. For species collectively, there was non-random community structuring, with two grids displaying more species aggregation than expected. While two grids had non-random co-occurrence patterns, three grids did not differ from random, which differs from that reported for mammalian taxa on average. Other small-mammal studies have documented species segregation, while this study detected more positive than negative associations. Similarities in preference and habitat use (or diet) are likely explanations for interspecific overlap patterns at stations and co-occurrence patterns among grids. Simultaneously evaluating associations of species pairs and all species on a grid collectively is novel methodology as applied to mammals, adding to understanding of species co-occurrence.

Key Words: mammalian communities, mark-and-recapture, null-models, pattern, species overlap

INTRODUCTION

For decades, co-occurrence of species has been a significant area of ecological research (Bowers & Brown 1982, Cole 1949, Diamond 1975, Hutchinson 1959, Kissell & Kennedy 1992, MacArthur & Levins 1967, Michael 1920), and understanding processes and factors that determine which species coexist within a community has been a long-standing goal in ecology (Cardillo & Meijaard 2010). The theory of limiting similarity (Hutchinson 1959, MacArthur & Levins 1967), in particular, stimulated interest in mechanisms influencing coexisting species. Knowing why species occur where they do is of intrinsic scientific interest, and such explanations may differ depending on the scale assessed. At local and microhabitat scales, persistence and coexistence of species can be influenced by environmental filtering through abiotic factors (e.g. temperature, availability of water) and biotic interactions (e.g. predators, prey, parasites), with density-dependent processes such as competition, disease and herbivory operating most intensively at neighbourhood scales (Cavender-Bares *et al.* 2009, McPeek & Brown 2000). A basic first step for elucidating mechanisms is to determine which species coexist and the nature of their coexistence. At present, co-occurrence of small mammals is not well understood, and assessments of multiple species occurring together seldom have been conducted.

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Null models represent an effective way to detect patterns of co-occurrence in a community (Gotelli 2000). While null-model analysis cannot determine factors responsible for aggregation or segregation of species, it can highlight non-random patterns of co-occurrence within a community (Rohde 2005).

Studies of small mammals on grids can serve as models for studying non-random distributional patterns of assemblages and for evaluating associations between pairs of species. Rodents of deserts of the south-western United States have been studied through field experiments and comparative geographic analyses (Brown *et al.* 2000). From those studies has emerged evidence that competition affects local abundance, limits local distributions and restricts membership in local communities to a subset of the regional pool of species (Brown *et al.* 2002).

Communities of small mammals in tropical dry deciduous forests in western Mexico have received relatively little attention. However, given the numerous endemic species in western Mexico and concomitant human-induced environmental changes occurring at a rapid pace, research on species assemblages becomes relevant for theoretical and conservation reasons.

Through mark-and-recapture studies of small mammals in Colima, Mexico, we had an opportunity, based on replicate grids, to quantify co-occurrence between pairs of species, as well as for all species in an assemblage simultaneously. The null hypothesis for each pair is that species are distributed independently of one another. For all species on a grid considered collectively, the null is that species are distributed randomly in their spatial environments. Alternative hypotheses predict non-random patterns of co-occurrence, which may be due to competition, predation and mutualism between particular pairs of species and among larger groups of species (Gotelli & Graves 1996). It has been suggested that species coexisting within local communities tend to be more evenly distributed among functional groups (based on dietary habits) than expected by chance (Brown *et al.* 2000, Fox & Brown 1993, 1995); if true, species associated with one another would be less likely to be from the same functional group. Evaluation of these suppositions can provide new information of value in determining the nature and degree of co-occurrence among small mammals.

METHODS

Study area and trapping

Data were collected in January 2004 during the annual dry season in coastal habitat adjacent to the Pacific Ocean at Playa de Oro, Colima, Mexico. Trapping locations were within 1 km of the ocean at altitudes less than 10 m asl and in tropical dry deciduous forest, with thorn-forest and mangrove elements. Prominent trees and shrubs included *Coccoloba barbadensis* Jacq., several species of *Acacia* including *A. hindsii* Benth. and *A. farnesiana* (L.) Willd., *Senna pallida* (Vahl) H.S. Irwin & Barneby, *S. occidentalis* (L.) Link, *Pithecellobium lanceolatum* (Willd.) Benth., *P. dulce* (Roxb.) Benth., *Hyperbaena ilicifolia* Standl., *Crataeva tapia* L., *Prosopis juliflora* (Sw.) DC. and *Guazuma ulmifolia* Lam. (Schnell *et al.* 2008). Grazing occurred in the area, but large portions of our grids were not accessible to livestock due to thickness of vegetation. Land in the area was agricultural, including groves of the coconut palm (*Cocos nucifera* L.).

Five non-overlapping trapping grids were established. Grids 1–5 were situated linearly along the coast (specific locations shown in Schnell *et al.* 2010: figure 1). Distances between adjacent grids (numbered sequentially 1–5) were 0.86, 1.95, 3.07 and 0.50 km. Grid 1 and 2 had a mixture of thorn forest and mangrove with some palms. Grid 3 was in thorn forest adjacent to a palm plantation. Grids 4 and 5 featured a mixture of grassy plots, palm trees and thorn forest near agricultural fields. While, not unexpectedly, there were some differences among grids, all were similar and represented the same basic habitat. Furthermore, grids were sufficiently close geographically that all species recorded potentially could have been present on all grids. Typically, days were warm and nights cool (January average for Manzanillo is 24.6 °C; Instituto Nacional de Estadística, Geografía e Informática 2005), with little day-to-day variation in temperature and no rain during our study.

Each grid consisted of 100 trapping stations (10 × 10 square grid), with adjacent stations 10 m apart. Two Sherman live traps (7.5 × 9.0 × 23.0 cm; H. B. Sherman Traps, Tallahassee, Florida, USA) baited with rolled oats were placed at each station; one trap was on the ground and the other 1–2 m above ground tied to a thin plywood platform (12.5 × 34.5 cm) attached to a tree or a shrub. Grids were sampled for eight nights each with the exception of grid 5 (9 nights), resulting in an overall sampling effort of 8200 trap-nights (1 trap-night = 1 trap set for 1 night). Sampling dates were 3–5 and 9–13 January on grids 1 and 4; 2–5 and 9–12 January on grids 2 and 3; and 2–5 and 9–13 January on grid 5. Traps were checked once each day beginning at dawn, rebaited as needed and left open for the full 24-h period. For each capture, we recorded species and station of capture, tagged the animal with uniquely numbered Monel No. 1 ear tags (National Band and Tag Company, Newport, Kentucky, USA) and released it at site of capture. Nomenclature follows Musser & Carleton (2005) except that we treat *Liomys* as part of *Heteromys* based on analyses presented by Hafner *et al.* (2007).

Data analyses

Data from the five grids were combined to determine percentage of trapping stations shared by pairs of species (interspecific overlap). Species present at 10 or more trapping stations (considering captures and recaptures) were included in analyses. Some individuals were captured at more than one station. For each pair of species, total number of shared trapping stations was tabulated. The expected number of shared traps was calculated as $500T_iT_j$, where T_i and T_j, respectively, were the proportion of the 500 trapping stations where species i and j were captured. We employed Fisher's exact test (BIOMstat for Windows 3.3s, Exeter Software, Setauket, New York, USA) to assess the degree to which pairs of species shared trapping stations.

Analyses of interspecific overlap were applied to data based on first captures of individuals and were repeated using information on both initial captures and recaptures of individuals. Results were essentially the same, and we report on analyses based on both initial captures and recaptures.

EcoSim software (Version 7.72. Acquired Intelligence Inc. and Kesey-Bear, Jericho, Vermont, USA. http://garyentsminger.com/ecosim.htm) was used to evaluate patterns of co-occurrence for all species within individual grids through null-model analysis. Numerous options are available in EcoSim for evaluating co-occurrence of species. Several options including SIM2, SIM4 and SIM8 were explored. However, herein we report only on results from SIM2; it has robust statistical properties and only limited additional insight would have resulted from inclusion of findings based on the other options. Furthermore, SIM4 and SIM8 tend to be error prone when analysing C-scores, the index we employed in our analyses.

For each grid, a presence–absence matrix was created, designating species (rows) as being present (1) or absent (0) at each of the 100 trapping stations (columns). Captures and recaptures of all 10 species were included in the analysis.

A C-score (Stone & Roberts 1990) was used as a quantitative index of co-occurrence and is based on chequerboard units (e.g. species A is present at location 1 and species B is absent, while at location 2, species A is absent and species B is present). For each pair of species in a matrix, the number of chequerboard units was calculated as $(R_i - S)(R_j - S)$, where R_i and R_j were the total number of stations where species i and j were present, respectively, and S was the number at which both species occurred (Gotelli & McCabe 2002). The C-score index for each grid was determined by finding the average number of chequerboard units for all pairs of species.

The statistical significance of the observed C-score for a grid was evaluated by comparing it against an expected value based on the mean C-score of 5000 simulated null communities. Random null communities were created by holding occurrences of species (row totals) fixed, while stations (column totals) were considered equiprobable. The algorithm used (SIM2) is well behaved with respect to Type I and II errors even in noisy datasets and is robust in conjunction with the C-score (Gotelli 2000). Simulated matrices that included stations where no species occurred (i.e. degenerate matrices) were retained. A significantly larger observed C-score index than expected suggests less co-occurrence of species (segregation), while a lower score indicates more co-occurrence (aggregation; Sarà *et al.* 2006).

For comparisons among grids and to compute two-tailed P-values, a standardized-effect size (SES) was considered for each grid. These were calculated as $(X_{obs} - X_{sim})/SD_{sim}$, where X_{obs} is the observed C-score, X_{sim} is the mean C-score from the 5000 simulated random matrices and SD_{sim} is the standard deviation of the C-scores in the simulated matrices (Gotelli & Rohde 2002). An SES-value greater than 1.96 indicates a non-random segregation of species, while one less than −1.96 identifies a non-random aggregation of species (Wittman *et al.* 2010).

RESULTS

Individual species pairs

Eight of 10 species captured (Table 1) were at 10 or more trapping stations and were included in the analysis of interspecific overlap between pairs of species. Four species (*Oryzomys couesi*, *Sigmodon mascotensis*, *Heteromys pictus* and *Tlacuatzin canescens*) were present on all grids, and *O. couesi* was consistently the most abundant species on grids (Table 1).

Given the proportion of trapping stations used by each of the eight species based on captures and recaptures, *O. couesi* shared significantly more trapping stations than expected with *S. mascotensis*, *Baiomys musculus* and *Peromyscus perfulvus* (Table 2). Significant positive associations also were noted for *B. musculus* with *S. mascotensis* and with *Reithrodontomys fulvescens*. Significant negative associations were detected only for *H. pictus*, which shared fewer stations than expected by chance with *O. couesi* and with *S. mascotensis*.

For the 28 pairs of species, deviations for 14 pairs were numerically greater than expected, 13 were lower and 1 pair (*S. mascotensis* and *T. canescens*) shared the exact number of stations expected (Table 2). Of the seven associations reaching statistical significance, five were positive (i.e. species pairs shared more trapping stations than expected by chance) and two were negative.

As indicated, each of our stations had an elevated and a ground trap. Of the eight most frequently encountered

Table 1. Abundance of each species on five grids at Playa de Oro, Colima, Mexico, in 2004. Number of individuals caught is indicated, with number of trapping stations where caught in parentheses. Species are ordered by total abundance.

Species captured	Grid					Total
	1	2	3	4	5	
Oryzomys couesi	63 (68)	98 (73)	22 (20)	74 (69)	75 (71)	332 (301)
Sigmodon mascotensis	17 (31)	9 (17)	3 (5)	25 (34)	30 (38)	84 (125)
Baiomys musculus	–	–	–	33 (36)	18 (20)	51 (56)
Heteromys pictus	2 (2)	2 (2)	11 (20)	3 (3)	6 (9)	24 (36)
Peromyscus perfulvus	–	15 (25)	–	–	–	15 (25)
Reithrodontomys fulvescens	–	–	1 (1)	13 (14)	–	14 (15)
Tlacuatzin canescens	1 (1)	3 (3)	3 (6)	4 (4)	2 (2)	13 (16)
Heteromys spectabilis	1 (1)	–	4 (5)	3 (4)	1 (2)	9 (12)
Osgoodomys banderanus	–	–	2 (3)	–	1 (1)	3 (4)
Nyctomys sumichrasti	–	1 (2)	–	–	–	1 (2)
Total	84 (103)	128 (122)	46 (60)	155 (164)	133 (142)	

Table 2. Evaluation of interspecific overlap (Fisher's exact test) in use of habitat by eight species of small mammal in 2004 at Playa de Oro, Colima, Mexico. Comparison of number of trapping stations shared relative to number expected by chance based on proportion of stations used by each species. First value in parentheses is number of stations where species was caught and second indicates percentage this represents of 500 trapping stations.

Species	Number of stations shared with comparison species		Deviation from expected	P
	Observed	Expected		
Oryzomys couesi (301; 60.2%)				
Sigmodon mascotensis	102	75.3	26.8	< 0.001
Baiomys musculus	44	33.7	10.3	0.003
Heteromys pictus	14	21.7	−7.7	0.008
Peromyscus perfulvus	23	15.1	8.0	< 0.001
Reithrodontomys fulvescens	11	9.0	2.0	0.423
Tlacuatzin canescens	10	9.6	0.4	1.000
Heteromys spectabilis	5	7.2	−2.2	0.235
S. mascotensis (125; 25.0%)				
B. musculus	27	14.0	13.0	< 0.001
H. pictus	2	9.0	−7.0	0.004
P. perfulvus	5	6.3	−1.3	0.643
R. fulvescens	2	3.8	−1.8	0.377
T. canescens	4	4.0	0.0	1.000
H. spectabilis	1	3.0	−2.0	0.310
B. musculus (56; 11.2%)				
H. pictus	3	4.0	−1.0	0.785
P. perfulvus	0	2.8	−2.8	0.097
R. fulvescens	7	1.7	5.3	< 0.001
T. canescens	2	1.8	0.2	0.697
H. spectabilis	3	1.3	1.7	0.141
H. pictus (36; 7.2%)				
P. perfulvus	1	1.8	−0.8	1.000
R. fulvescens	0	1.1	−1.1	0.615
T. canescens	2	1.2	0.8	0.322
H. spectabilis	2	0.9	1.1	0.211
P. perfulvus (25; 5.0%)				
R. fulvescens	0	0.8	−0.8	1.000
T. canescens	1	0.8	0.2	0.566
H. spectabilis	0	0.6	−0.6	1.000
R. fulvescens (15; 3.0%)				
T. canescens	0	0.5	−0.5	1.000
H. spectabilis	1	0.4	0.6	0.309
T. canescens (16; 3.2%)				
H. spectabilis (12; 2.4%)	2	0.4	1.6	0.053

Table 3. Co-occurrence of species compared to null models on five grids at Playa de Oro, Colima, Mexico, in 2004.

	Grid				
	1	2	3	4	5
Observed C-score	21.6	53.1	49.4	129.2	79.3
Simulated C-score	64.4	86.9	48.2	151.9	97.4
$P_{(\text{two-tailed})}$	0.002	0.009	0.734	0.080	0.101
SD of simulated C-score	14.10	13.03	3.59	13.00	11.10
Standardized effect size (SES)	−3.03	−2.60	0.34	−1.75	−1.64

species, percentages of total captures in elevated traps were as follows: *O. couesi* (54%), *S. mascotensis* (16%), *B. musculus* (6%), *H. pictus* (5%), *P. perfulvus* (91%), *R. fulvescens* (59%), *T. canescens* (69%) and *Heteromys spectabilis* (8%). Thus, of those species that significantly co-occurred at trapping stations, most pairs included one species that was captured about equally in elevated and ground traps (*O. couesi* or *R. fulvescens*) coupled with a second species predominately using either ground traps (*S. mascotensis* or *B. musculus*) or elevated traps (*P. perfulvus*). For one pair (*S. mascotensis* and *B. musculus*) of co-occurring species, both were captured primarily in ground traps.

All species examined simultaneously

One also can assess whether co-occurrences of all species on a grid (considered collectively) are non-randomly structured. Two of the five grids had lower C-scores ($P < 0.05$) than expected by null models (negative SES-values; Table 3), indicating that species on average were aggregated at the trapping-station level more than expected. For grids 3–5, observed C-scores were not significantly different from simulated index values, suggesting that collective co-occurrence among small mammals on those grids was not structured.

DISCUSSION

The most important factor influencing distributions and abundances of small mammals within their geographic ranges probably is suitable habitat (Geier & Best 1980). In Jalisco, *O. couesi* and *B. musculus* reflected more similar use of habitat with each other than with any of 12 other species of small mammals studied (Ceballos Gonzalez 1989). In Colima, we noted that these two species had significant overlap in occurrence. Specific microhabitat preferences have been documented for several species in coastal Colima. Both *B. musculus* (Schnell *et al.* 2008) and *S. mascotensis* (Schnell *et al.* 2010) preferred open areas with more forbs, grasses and woody plants; herein, we demonstrated a significant positive association between these two species.

The differential use of vegetation in a vertical dimension was judged by Ceballos Gonzalez (1989) to be a leading mechanism of coexistence for small mammals within the semideciduous forests of Jalisco. He calculated the number of captures at ground and elevated levels; overall differences were present among the five most abundant species (*H. pictus*, *P. perfulvus*, *O. melanotis*, *Osgoodomys banderanus* and *Xenomys nelsoni*). Our study lends partial support for differential vertical use by species in that there was some partitioning in a vertical dimension but some overlap as well. Four of the five overlapping pairs included a species that was captured about equally in ground and elevated traps, with the other species being almost exclusively in ground or elevated traps. One pair (*S. mascotensis* and *B. musculus*) consisted of species that both predominately used ground traps; thus, vertical partitioning of habitat likely is not the primary mechanism fostering co-occurrence on our grids.

Five of the significant pairwise associations in our study were positive, with two negative associations involving *H. pictus*. Schnell *et al.* (2010) reported co-occurrences of species concerning *S. mascotensis* for the same grids, finding that, although *H. pictus* and *S. mascotensis* occurred together on the same grids, they were using habitats in different ways. Our present analysis confirms those observations and, additionally for *H. pictus*, indicates that it and *O. couesi* also were distributed differentially among trapping stations.

In tropical semideciduous forests of Tamaulipas, no difference in use of microhabitats was detected between *O. couesi* and *Heteromys irroratus* (Castro-Arellano 2005), a congener of *H. pictus* present on our grids. However, *O. couesi* and *H. irroratus* had an essentially opposite pattern of temporal overlap (Castro-Arellano & Lacher 2009). *Oryzomys couesi* was active primarily from 19h00–23h00, while *H. irroratus* was active from 02h00–05h00. In our study, *O. couesi* and *H. pictus* were frequenting different microhabitats. It would be of interest to investigate temporal overlap of *O. couesi* and *H. pictus* in Colima.

Coexistence is theorized to be fostered through differential niche occupancy, and diet often is considered an important determinant of habitat use. Unlike other species in this assemblage, *H. pictus* is a heteromyid, a group known to rely heavily on seeds gathered from the ground (Briones & Sánchez-Cordero 1999). Individuals of *H. pictus* must routinely gather sufficient quantities of food to avoid rapid loss of mass (Sánchez-Cordero & Fleming 1993); thus, this species likely is inhabiting areas of the grid that are relatively rich in seeds – areas not regularly used by species with more generalized diets.

Fox & Brown (1993, 1995) assessed composition of rodent communities relative to functional group, which was defined based on diet and foraging. They hypothesized that species more similar in functional group tended to coexist less frequently in local communities. More particularly, the difference between numbers of species present in any two functional groups within a community typically differed by no more than one; such assemblages are termed favoured states. For example, in the case of three functional groups (e.g. granivore, herbivore and omnivore), communities in which these groups contain 1-2-1 or 3-3-4 species are in a favoured state, whereas those with 1-2-0 or 3-3-5 species are in an unfavoured state. In our study, four of the six species involved in significant associations would be classified in an omnivorous functional group, including *O. couesi* (Medellín & Medellín 2005), *B. musculus* (Sánchez-Cordero 2001), *P. perfulvus* (Ceballos & Miranda 2000) and *R. fulvescens* (Vázquez *et al.* 2004). *Sigmodon mascotensis* would be in a herbivorous functional group and *H. pictus* in a granivorous functional group (Sánchez-Cordero 2001). Of the five pairs of species with significant overlap in our study, only two pairs had members from different functional groups (herbivore and omnivore), and three pairs consisted of members from the same functional group (omnivore). When comparing number of species present in each functional group for a grid, only one grid featured a favoured state. Overall, our results offer little evidence for the role of functional group in structuring assemblages within communities.

When analysing co-occurrence of all species collectively, two grids had more co-occurrence of species than predicted by random expectation. Percentages of shared stations between individual pairs of species partially explain results of the analysis for all species collectively. For example, on grid 1 and 2, species collectively were aggregated and the two most-abundant species (*O. couesi* and *S. mascotensis* on grid 1, and *O. couesi* and *P. perfulvus* on grid 2) exhibited strong overlap in stations used. Grid 3 was the only grid where the two most-abundant species (*O. couesi* and *H. pictus*) were negatively associated. No study has examined whether associations between small mammals differ with changing seasons (e.g. wet versus dry) and, as previously mentioned, most research on co-occurrence of small mammals has concerned species in temperate deserts, with little attention given to tropical woodlands. Our study was conducted during the dry period at a locality with pronounced wet-dry seasonality. It would be an ideal location for investigating the effect, if any, of seasonality on species co-occurrence.

Gotelli & McCabe (2002), Gotelli & Rohde (2002) and Rohde (2005) suggested body size, population size, dispersal ability or a combination of these to be determinants of whether animals are subject to structuring mechanisms (e.g. competition) affecting overall patterns of co-occurrence. They considered a continuum with one end being small-bodied taxa that tended to show random co-occurrence and weak vagility and/or small population size; this contrasted with the other end of large-bodied taxa exhibiting predominantly non-random co-occurrence and high vagility and/or large population size.

One reason proposed for the existence of such a trend in degree of co-occurrence is that ecological niches of larger animals have higher energy requirements and greater niche saturation, resulting in interspecific interactions being stronger and more likely to influence structure of communities. When comparing deviations from randomness (average SES), taxonomic groups were partitioned in part along this continuum into random patterns (< 2) in poikilotherms (fish ectoparasites 0.4, amphibians and reptiles 1.3, non-ant invertebrates *c.* 1.3) and non-random patterns of segregation (> 2) in homeotherms (non-volant mammals 3.1, birds 3.6, bats > 4), with ants (2.6) being the exception to the pattern (Gotelli & McCabe 2002, Gotelli & Rohde 2002). Two of our five grids exhibited SES-values of −3.0 and −2.6 (aggregation), a result nearly opposite that reported for mammals as a whole. Our remaining three grids produced SES-values that did not differ from random expectation. The average SES-value for all grids (–1.74) was random.

One possible explanation for our finding being different from that of Gotelli & McCabe (2002) for mammals is that we analysed data at a localized level, while most of the mammalian assemblages in their work were based on datasets amalgamated for larger geographical areas. Historically, analyses of co-occurrence have been applied to larger spatial scales, but highly non-random structure has been exhibited at both the local and broader geographic levels (Brown *et al.* 2000). As was amply illustrated over two decades ago by Wiens (1989) and others, ecological patterns of occurrence are not independent of the spatial scale on which they are viewed. We should expect co-occurrences often would differ when evaluated at different spatial scales.

We found more positive than negative associations between pairs of species and aggregation on grids. Non-random negative patterns of co-occurrence have been detected for desert rodents (Bowers & Brown 1982), where size of body was implicated as having a significant role in co-occurrence for granivorous species, with significant negative associations between species of similar size.

However, when species from different trophic guilds were combined in the same analysis, patterns of species co-occurrence were no longer non-random. Consequently, Bowers & Brown (1982) warned that when an entire community is examined without regard to guild structure, apparently random associations between species in different guilds may obscure deterministic patterns of coexistence within guilds. Our null-model analysis of co-occurrence included all species present on a grid regardless of guild. Despite this, significantly non-random patterns in co-occurrence were exhibited on two grids.

Our analysis rejected the null hypothesis and demonstrated significant interspecific overlap for multiple pairs of species. Similarities in preference and use of habitat (or diet) are the most likely explanations for patterns of interspecific overlap at trapping stations between pairs of species. There is little evidence that members of similar functional groups coexist less frequently in local communities. Other studies confirm some of the associations between pairs of species that we detected. Null-model analysis provided evidence for structuring of communities, with some grids displaying non-random co-occurrence for all species collectively. However, for all grids averaged together, our results did not deviate from random as they did for mammals on average, suggesting that not all mammalian communities fit well into the continuum described by Gotelli & McCabe (2002), Gotelli & Rohde (2002) and Rohde (2005). The creation of non-random patterns of co-occurrence among grids might be the result of interactions among species, including interspecific facilitation or shared preferences (Krasnov *et al.* 2006, 2010). The two grids with significantly more co-occurrence than expected had a similar mix of habitats, with thorn forest, mangrove elements and some palm trees.

Overall, we were able to quantify interspecific overlap between each pair of species in an assemblage and perform rigorous statistical tests on those associations. In addition, our study has approached the issue of co-occurrence of small mammals by evaluating multiple species in an assemblage simultaneously, with replication, using null models. Investigating associations between pairs of species in combination with analyses of all species on a grid considered collectively is a novel methodology as applied to mammals that adds to our understanding of co-occurrence of species.

ACKNOWLEDGEMENTS

We thank the numerous students from the United States and Mexico who assisted in fieldwork and Esteban Meneses for help in facilitating our studies of mammals in Colima. In addition, we appreciate helpful comments and suggestions on the manuscript from Michael A. Mares, Ingo Schlupp and an anonymous reviewer. Permits for conducting this investigation were provided by the Instituto Nacional de Ecología, Dirección General de Vida Silvestre FAUT.0103 to Cornelio Sánchez-Hernández. Voucher specimens were deposited in the Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, and Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México.

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