Lack of Interspecific Interactions of Everglades Rodents on two Spatial Scales

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Peromyscus gossypinus, *Sigmodon hispidus* and *Oryzomys palustris* are the co-dominant rodents that inhabit the Everglades of south Florida, USA. Here the three species occur micro-sympatrically at extremely high densities on small discrete habitat islands of high species richness of hammock vegetation that dot the Everglades sawgrass prairie. A long term live-trapping study was conducted to determine whether the species were distributed independently of one another. Data are analyzed on two spatial scales. First, among hammock islands there was no evidence of complementarity (an increase in the population of one species negatively affecting the density of another) between all combinations of species pairs. Second, there were two noticeable vegetative zones on the hammock islands. While preferences between zones were demonstrated by each rodent, it appeared that the distribution of each species on hammocks was independent of the presence of the other species. Space is considered to be an important niche dimension in rodents, yet these data do not reject the hypothesis that local and regional densities of the species on hammocks are independent.

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I. INTRODUCTION

Of concern to geographical ecologists is the extent to which competition may modify regional and local coexistence of populations (Mac-Arthur, 1972). Competitive interactions between species may be either active (interference competition) or passive (exploitative competition). Either may result in a reduction of local density of one or both micro-sympatric populations, the local exclusion of one population, or a division of the potential range of resources within a habitat. Throughout 1975—1977 I conducted a live-trapping (mark-recapture) study of the spatial dynamics of three sympatric rodents *Peromyscus gossypinus* (LeConte, 1853), *Sigmodon hispidus* Say & Ord, 1825, and *Oryzo-*

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mys palustris (H a r l a n, 1837), in the Everglades of south Florida, USA. In this paper I examine evidence for competition among the three species on two spatial scales: between and within patches of habitat. The patches of suitable habitat are small and the densities of each species living on them high, hence conditions were favorable to demonstrate interactions among the species. Instead, the data indicate that each species is distributed indepentently of the others.

II. STUDY SITE

The study area is located in Taylor Slough at the southeastern edge of the Davis Everglades region (D a v i s, 1943). Here the flat sawgrass prairie is punctuated by tree islands called hammocks. Hammocks are composed of a high diversity of trees (most have at least 15 species of co-dominant tropical and subtropical trees), and are structurally complex (S m i t h & V r i e z e, 1979). A single tree species, cocoplum, occupies low-lying wet areas, primarily around the edges of hammocks. Hence, the habitat provides two interesting contrasts: 1) prairie and hammock which differ markedly in habitat structure; and 2) interior hammock vegetation and cocoplum fringe which differ markedly in species diversity (but not greatly in structure).
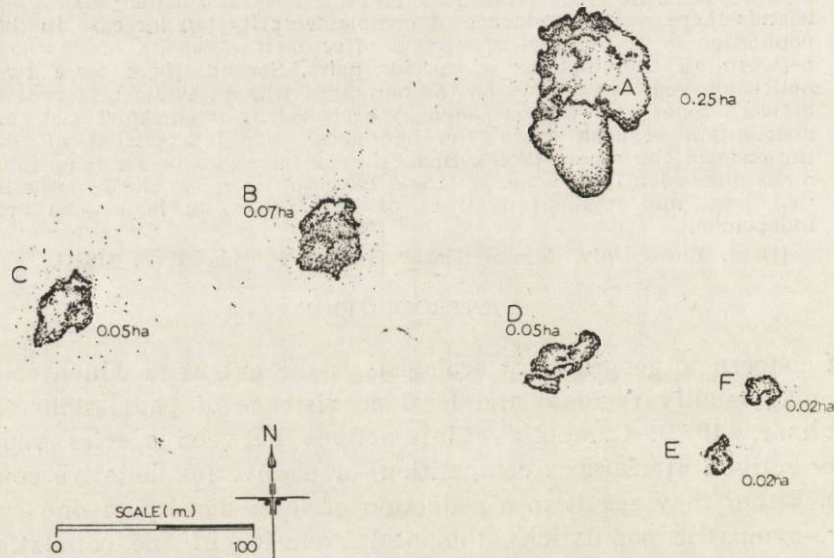

Fig. 1. Map of the study area showing size and spacing of the hammocks.

The seasonal nature of rainfall in south Florida provides an additional important contrast on the study area. In the summer wet season (June—November) the prairie is flooded and the tree islands are the only high (0.5—1.0 m above the water level) ground available to rodents. In the winter dry season (December—May) the prairie becomes a dusty plain and is available for continual occupancy.

Trapping was conducted on a series of 6 hammocks which varied in size and

distance from one another (Fig. 1; Table 1). This constellation of hammocks was relatively isolated from other similar hammocks in the area.

III. METHODS

Traps were set in grids conforming to the shape of each hammock. Inter-trap distance was 4 m on Hammock A and 3 m on Hammocks B—F. Table 1 shows the number of traps set on each hammock and its size. Densities are based on the sum of areas of the hammocks and the minimum number of individuals known to be alive (*MNA*) for the study area within each trapping session. Estimates of trappability were high (greater than 0.96 following method of K r e b s *et al.*, 1976), hence these density estimates are reliable (S m i t h & V r i e z e, 1979). Traps were set on each hammock for two nights in each trapping session. Dry season trapping sessions extended from 28 January — 12 June 1975 (4 sessions), 19 February — 20 May 1976 (3 sessions), and 23 February — 7 May 1977 (2 sessions).

Table 1

Characteristics of the hammocks.

Hammock	Area (ha)	Number of Traps	Percent Traps	
			in Cocoplum	in Hammock
A	0.25	112	0.54	0.46
B	0.07	64	0.55	0.45
C	0.05	52	0.54	0.46
D	0.05	52	0.52	0.48
E	0.02	26	0.50	0.50
F	0.02	23	0.61	0.39
Total	0.46	329	0.54	0.46

Wet season trapping sessions extended from 3 August — 22 November 1975 (4 sessions), 24 June — 29 October 1976 (3 sessions), and 19 September — 2 December 1977 (2 sessions).

Each trap placement on the hammocks was tallied as being either in habitat of exclusive cocoplum or in habitat comprised of a high diversity of other hammock trees (hereafter termed »hammock«). The ratio of traps in cocoplum versus hammock was fairly constant among Hammocks A—F (Table 1). The high proportion of cocoplum trap placements is largely a function of edge effect: these are small habitat islands with relatively large perimeters.

To determine complementarity (an increase in the population of one species negatively affecting the density of another) for each species pair I used data for 5 trapping sessions (3 June — 22 November 1975) when the density of each species was high. Population levels of individual hammocks were tabulated as either increasing or decreasing from the previous trapping session. If the population level remained the same it was considered increasing because it was not negatively affected by the presence of the other species. If no individuals were caught in consecutive trapping sessions on a hammock, the level was tabulated as decreasing. Data from Hammocks A and C in two trapping sessions were not used because of raccoon disturbance.

IV. RESULTS AND DISCUSSION

1. Population Dynamics

Peromyscus tend to occupy the hammocks year-round; *Sigmodon* and *Oryzomys* in the wet season only. In the dry season *Sigmodon* disperse in to the prairie surrounding the hammocks, while *Oryzomys* (the most aquatic of the three species), leave the study site presumably to refuge in more mesic site farther west in the Everglades (S m i t h & V r i e z e, 1979). While the data originate from mice caught on hammocks, individuals of each species foray frequently among hammocks (S m i t h & V r i e z e, 1979). The reproductive pattern for each species, established from 1975—1976 data, was to breed on the hammocks during wet seasons (S m i t h & V r i e z e, 1979).

Table 2

Average density (*MNA*)/hectare.
MNA — minimum number of individuals known to be alive.

Year and Season	Peromyscus	Sigmodon	Oryzomys
1975			
Dry Season	133.2	22.8	4.9
Wet Season	119.0	59.8	36.4
1976			
Dry Season	159.4	8.0	2.2
Wet Season	37.8	3.6	28.3
1977			
Dry Season	155.4	10.9	8.7
Wet Season	76.0	10.9	19.7

Peromyscus densities were high at all times except the wet seasons of 1976 and 1977 (Table 2). The low density in 1976 was caused by in-trap mortality by predatory raccoons, *Procyon lotor* S t o r r, 1780, at the end of the 1976 dry season. The relatively low density in 1977 was caused by the unusual failure of the population to reproduce at that time (S m i t h, in preparation). These densities of *P. gossypinus* are high. Normal peak densities taken from long-term studies throughout the range of the species average 2—6/hectare (reviewed in S m i t h & V r i e z e, 1979).

Sigmodon densities on the hammocks were highest in the wet season of 1975, but the raccoons were successful also at limiting the population size of *Sigmodon* in 1976 (S m i t h & V r i e z e, 1979); they inexplicably failed to attain high densities in the wet season of that year and 1977 (Table 2). In the 1975 dry season *Sigmodon* were commonly trapped in the prairie and most of these individuals also visited hammocks, hence the relatively high hammock densities reported at this time. The density

attained by *Sigmodon* throughout the wet season of 1975 is significantly higher than that which is normally reported for the species throughout its range (S m i t h & V r i e z e, 1979; L a y n e, 1974).

Oryzomys were trapped on the hammocks at high densities throughout the wet season of each year (Table 2). Although wet season density was lowest in 1977, this figure is still higher than the peak density (17.8/ha) reported in the literature (N e g u s *et al.*, 1965). Apparently *Oryzomys* were unaffected by raccoon predation because they had not yet dispersed on to the study site at the time of this disturbance.

In summary, the three species bred synchronously on the hammocks and were each at high density in the wet season of 1975. During other seasons and years there were varying combinations of densities of the three species.

2. Patch-patch Interactions

H o r n & M a c A r t h u r (1972) and S l a t k i n (1974) explored theoretically the dynamics of patchy systems and determined that species

Table 3

Complementarity of hammock occupation by *Peromyscus*, *Sigmodon* and *Oryzomys*. Data are from 5 trapping sessions when densities of each species on the study area were high (only 3 trapping sessions were used for hammocks *A* and *C* due to trap disturbance). For each species pair population levels of individual hammocks were tabulated as increasing or decreasing from the previous trapping session.

	Hammock							Avg. change (no. of individuals)		
---	A	B	C	D	E	F	Σ	Peromyscus	Sigmodon	Oryzomys
Peromyscus increases; *Sigmodon* increases	2	3	0	1	1	2	9	+2.9	+3.7	
Peromyscus increases; *Sigmodon* decreases	0	0	1	1	1	1	4	+4.0	−1.3	
Peromyscus decreases; *Sigmodon* increases	0	1	2	1	3	1	8	−3.0	+1.9	
Peromyscus decreases; *Sigmodon* decreases	1	1	0	2	0	1	5	−2.2	−1.2	
Peromyscus increases; *Oryzomys* increases	2	2	1	2	0	1	8	+3.6		+2.6
Peromyscus increases; *Oryzomys* decreases	0	1	0	0	2	2	5	+1.8		−1.0
Peromyscus decreases; *Oryzomys* increases	1	1	1	1	2	1	7	−3.3		+2.7
Peromyscus decreases; *Oryzomys* decreases	0	1	1	2	1	1	6	−2.0		−1.0
Sigmodon increases; *Oryzomys* increases	2	2	1	2	2	1	10		+3.5	+2.8
Sigmodon increases; *Oryzomys* decreases	0	2	1	1	2	2	8		+1.7	−0.8
Sigmodon decreases; *Oryzomys* increases	1	1	1	1	0	1	5		−1.2	+1.8
Sigmodon decreases; *Oryzomys* decreases	0	0	0	1	1	1	3		−2.3	−1.0

could exclude one another on patches but remain extant regionally if colonization rates between patches exceeded extinction rates on patches. Initially I felt that the Everglades hammock-rodent system would provide a useful test of these models based on the small sizes of the hammock islands (Table 1) and the low expected densities reported from the literature on other populations of the same species. Instead, there was no evidence that regionally any of the species were influenced by the presence of the others (Table 3). This analysis of complementarity shows that *Peromyscus* increased more times during periods when *Sigmodon* and *Oryzomys* were increasing than when they were decreasing. *Sigmodon* and *Oryzomys* each increased more while the other was also increasing. Further, in 4 of 6 cases the magnitude of population changes was greater if both species of a pair were each increasing than if one were negatively affecting the population level of another (Table 3). In conclusion, not only were no extinctions on patches (hammocks) observed, but population levels of each species appeared independent of each other.

3. Within-patch Interactions

Given that there was no complementarity of densities of the three species among hammocks, if competition were to occur between the species it must be for resources available on the hammocks and result in a subdivision of that resource. Because space is known to be an important niche dimension in rodents (G r a n t, 1972), I examined the spatial dynamics of the populations within the hammocks to determine whether or not the local (or point) densities and distributions of each species were independent or the result of competition. Although none of the data are directly experimental, there are several important contrasts (temporal and spatial) which can be used to differentiate among the responses of each species.

Table 4 shows the utilization of habitat (cocoplum versus hammock) by species for each season. Data were summed for all hammocks because 1) sample sizes on individual hammocks were generally too small to yield significant results; 2) changes in density of each species within each season were synchronous; and 3) the mechanisms of habitat selection and/or interspecific interactions were assumed to be equal on all hammocks.

The utilization of habitat (cocoplum versus hammock) by each species for each season is given in Table 4. These data were analyzed using the G statistic of S o k a l and R o h l f (1969, p. 576). G_h tested for heterogeneity among samples; G_p, for goodness of fit to the expected random distribution of captures based on the proportion of traps set in

each of the two habitat types (Table 1). Data for *Peromyscus* were analyzed by season because there was significant heterogeneity among samples from all season $G_h = 48.79$, $p > .01$). Data were homogeneous among trapping sessions within both wet ($G_h = 4.04$, $p > .05$) and dry ($G_h = 5.70$ $p > .05$) seasons. *Peromyscus* were not distributed randomly on hammocks during either the wet or dry season. In the wet season 58% of captures were in hammock vegetation; in the dry season 60% of captures were in cocoplum. Each of these shifts in habitat utilization is significant (wet season: $G_p = 25.74$, $p < .01$; dry season: $G_p = 13.32$, $p < .01$).

Both *Sigmodon* and *Oryzomys* demonstrated homogeneity among all seasons (*Sigmodon*: $G_h = 8.08$, $p > .05$; *Oryzomys*: $G_h = 6.60$, $p > .05$). Further, each of these species preferred cocoplum habitat; 71% of all *Sigmodon* captures were in cocoplum, 78% of all *Oryzomys* captures were in cocoplum. Each of these habitat preferences is significant (*Sigmodon*: $G_p = 28.50$, $p < .01$; *Oryzomys*: $G_p = 55.71$, $p < .01$).

Table 4

Habitat occupancy on hammocks by *Peromyscus*, *Sigmodon* and *Oryzomys* by season and year. Percent of total number of captures are in parentheses.

Species	Trapping Session	Number of captures	
		Cocoplum	Hammock
Peromyscus	1975 dry	202 (57)	150 (43)
	1975 wet	102 (38)	165 (62)
	1976 dry	224 (65)	121 (35)
	1976 wet	31 (46)	37 (54)
	1977 dry	110 (56)	85 (44)
	1977 wet	51 (49)	53 (51)
Sigmodon	1975 dry	43 (78)	12 (23)
	1975 wet	87 (66)	44 (34)
	1976 dry	3 (100)	0 (0)
	1976 wet	3 (50)	3 (50)
	1977 dry	13 (87)	2 (13)
	1977 wet	16 (73)	6 (27)
Oryzomys	1975 dry	9 (100)	0 (0)
	1975 wet	75 (78)	21 (22)
	1976 dry	1 (50)	1 (50)
	1976 wet	60 (77)	18 (23)
	1977 dry	9 (90)	1 (10)
	1977 wet	16 (73)	6 (27)

In summary, despite the small size of the hammocks and the close inter-trap distances, a definite pattern of habitat utilization was found. In the dry season each species tended to use the cocoplum habitat, but in the wet season, *Peromyscus* shifted its habitat use to the center of hammocks.

Because of the varying densities of the species among seasons and

years, several interspecific comparisons of habitat utilization are possible. First, in the 1975 dry season *Peromyscus* occupied the hammocks concurrently with a relatively high population of *Sigmodon*, yet both preferentially occupied the cocoplum fringe. In 1976 and 1977 the *Sigmodon* density was considerably less than in 1975, and *Peromyscus* again showed preference toward the cocoplum habitat.

Second, a significant habitat shift did not occur in *Sigmodon* between the 1975 dry season (when they coocurred only with *Peromyscus*) and the 1975 wet season (when they coocurred with high densities of *Peromyscus* and *Oryzomys*).

Third, there was no difference in the degree of habitat preference demonstrated by *Oryzomys* among wet seasons, yet in 1975 there were high densities of both other micro-sympatric species, in 1976 both micro-sympatric species were low in density, and in 1977 *Peromyscus* was relatively high in density, while *Sigmodon* was low. *Oryzomys* appeared to favor the cocoplum independent of the presence or absence of other species.

While not all possible pairs of comparisons can be made with the available data, it seems clear that the presence, and habitat occupancy of the three species appeared to be independent in most cases. The only possible case of habitat displacement was the shift of *Peromyscus* to the center or highground of hammocks after colonization by *Sigmodon* or *Oryzomys* at the beginning of the wet season.

Coexistence on hammocks may also be achieved by utilizing different food resources. I have not yet tested this niche dimension (although each species is known to eat a wide variety of food types (N e g u s *et al.*, 1961; S h a r p, 1967; S m i t h, 1975; W o l f & L i n z e y, 1977) and hence may have a high potential for food overlap with each other). Each species may also forage in the prairie and not rely exclusively on food resources on the hammocks. Even if this is the case, however, my data originate from animals caught on hammocks, and the problem of absolute crowding and the behavior which allows this remains. Further, while the data show strong habitat preference in all three species, there were still many captures made in the non-preferred habitat of each species. This fact plus the high density of each species in the 1975 wet season and the small size of the hammock islands argue convincingly that these species cannot completely avoid one another.

P. gossypinus is known to be arboreal (L a y n e, 1970, present study), and this behavior may alleviate some of the population pressure by utilizing a vertical spatial dimension on the hammocks. I do not know if the frequency of this behavior increases in the wet season after the larger rats have colonized the hammocks. M'C l o s k e y & F i e l d w i c k

(1975) reported that *P. leucopus* (R a f i n e s q u e, 1818) showed the same degree of arboreality in the presence and absence of *Microtus pennsylvanicus* (O r d, 1815).

If competition between micro-sympatric rodents occurs, its effects should be most noticeable under conditions of high density. As outlined above, densities of each species on the hammocks reached levels higher than those reported from other studies throughout the geographical range of each species. The present data do not reject the hypothesis that local and regional densities of the species on the hammocks are independent. Working with micro-sympatric *P. leucopus* and *M. pennsylvanicus* M'C l o s k e y (1975) also concluded that overt interspecific interactions may play a minor role in their local distributions. It will take replicated field experiments to test the ideas suggested by the data this initial study of rodents on the hammock islands.

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MIĘDZYGATUNKOWE WSPÓŁZALEŻNOŚCI U GRYZONI ŻYJĄCYCH
NA BAGNACH

Streszczenie

Peromyscus gossypinus, Sigmodon hispidus i *Oryzomys palustris* są współdominującymi gryzoniami zamieszkującymi bagna południowej Florydy. Stwierdzono, że te trzy gatunki występują sympatrycznie w niezwykle wysokim zagęszczeniu na małych (0,02—0,25 ha) wysepkach (Ryc. 1), różniących się wyraźnie bardzo bogatym składem florystycznym od otaczającej roślinności trawiastej. Odłowy prowadzono przy pomocy pułapek żywołownych w celu określenia czy gatunki były rozmieszczone niezależnie od siebie (Tabela 1). Stwierdzono po pierwsze, że na wysepkach wzrost liczebności jednego gatunku nie powodował zmniejszenia liczebności drugiego gatunku (Tabele 2, 3); po wtóre, były tam dwie wyraźne strefy roślinności, różnie preferowane przez każdy gatunek gryzonia (Tabela 4).