

# Utilization of a habitat mosaic by cotton rats during a population decline

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## Abstract

This study describes the demographic features of a population of *Sigmodon hispidus* utilizing the habitat mosaic provided by a Carolina Bay on the Atlantic coastal plain of South Carolina. A total of 71 cotton rats were captured 160 times on a 4 ha grid during a winter decline from 25/ha to less than 1/ha. Body weights of adults declined until early February and then increased; those of subadults grew very slowly until February followed by a spurt in growth. Weight gain did not differ between survivors and non-survivors for males, but female survivors gained 1.5 g per week more than non-survivors. Female subadults exhibited higher mortality early in the decline and males later.

Adult females were randomly distributed across 8 microhabitats, whereas adult males were almost exclusively confined to heavy *Rubus* cover. Subadult males used wet sites more than any other cohort; subadult females were widely distributed using drier sites most frequently. By the end of the decline, all survivors were localized in *Rubus*-dominated patches. No statistically significant changes in electromorph genotypes or allele frequencies were detected, but survivors had a higher frequency of the F-allele at the adenylate kinase locus than did non-survivors (42.3% vs. 16.7%).

Our findings affirm the importance of a landscape perspective in understanding the population dynamics of cotton rats, and show how a habitat mosaic influences survival differentially among sex-age cohorts.

## 1. Introduction

In recent years, the study of small mammal ecology has moved into the realm of landscape ecology. Following the early lead of Soviet ecologists (for reviews see Anderson 1970; Lidicker 1985), and the insightful paper by Hansson (1977), researchers have come to appreciate the critical importance of habitat mosaics in influencing the lives of organisms, including species of small mammals. The spatial array of micro-habitats in which organisms commonly live influence their success through variations in patch size, quality, connectedness, and

presence of competitors, predators, and parasites.

This research utilized the habitat mosaic provided by a Carolina Bay on the Atlantic coastal plain. This bay provides a moisture gradient from open water to dry sand, a variety of soil conditions, and cover features varying from open grass to thick shrubs and some trees. The small mammal community on the site consists of at least six species (Golley *et al.* 1965), the largest of which is the cotton rat, *Sigmodon hispidus*. We chose the cotton rat as our focal species because it is a habitat generalist (Golley *et al.* 1965; O'Farrell *et al.* 1977; Kincaid and Cameron 1985), a herbivore with relatively small

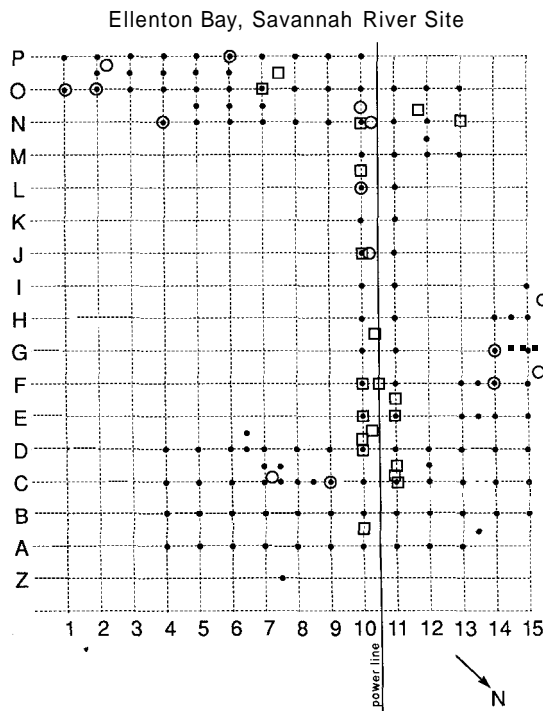
home range (Goertz 1964; Wiegert and Mayenschein 1966), and is the most common species other than the short-tailed shrew (*Blarina brevicauda*). Previous research with cotton rats has shown that micro-habitat utilization is selective and may vary seasonally (Goertz 1964; Kincaid and Cameron 1985; Kincaid *et al.* 1983; Odum 1955; Wiegert and Mayenschein 1966), and that sex and size differences may occur (Spencer and Cameron 1983).

The study covered a period of population decline from the end of one breeding season to the beginning of the next. We reasoned that a population undergoing a decline would be more environmentally stressed than one in an increase phase, and hence micro-habitat utilization patterns might become more evident, and would be unencumbered by the complexities of reproduction. Our objectives were to: 1) monitor micro-habitat utilization in the cotton rat by sex, age, and past reproductive history; 2) search for interspecific influences; and 3) measure survivorship as a function of micro-habitat, body weight trends, and electromorph genotype. We sought to improve our understanding of how such species utilize and respond to habitat heterogeneity.

## 2. Study area

The study site was located at Ellenton Bay, a Carolina Bay (Shalles *et al.* 1989), located at the Savannah River Site in Aiken County, South Carolina. The Bay covers approximately 11.3 ha with water varying in depth between 0 and 1.3 m and ranging from 0 to 10 ha depending on season and rainfall. When our study began in late November, 1989, there was less than 20 cm of water in the Bay covering less than 1 ha, and by the end of the study in March, 1990, the depth had increased to 50 cm and covered approximately 7 ha.

The Bay vegetation is concentrically arranged. Flooded areas are dominated by *Nymphaea odorata* (water lily) and the grass *Panicum hemitomon* with patches of the rush *Juncus canadensis*. Around this, in areas seasonally or occasionally flooded, is a band of almost pure *Panicum* but with significant presence of *Eupatorium capillifolium*



**Fig. 1.** The trapping grid at Ellenton Bay, Savannah River Site. Twelve temporary sites are shown along with the permanent grid locations. Estimated centers of activity for 20 adult male ( $\square$ ) and 16 adult female ( $\circ$ ) cotton rats, winter 1989–90 are also shown.

and *Erianthus giganteus*. Next there is a narrow band of these species dominated by *Andropogon virginicus* (broom sedge). Above this lies a thinner cover of *Panicum hemitomon* mixed with *Rhexia mariana* (meadow beauty) and *Rubus betulifolius* (blackberry). In drier sites extending up to the sand rim of the bay are shrubs and small trees, particularly *Cephalanthus occidentalis* (buttonbush), blackberry, *Liquidamber styraciflua* (sweet gum), *Prunus angustifolium* (Chickasaw plum), *P. serotina* (black cherry), and *Acer rubrum* (red maple). Along the south and west edges of the bay are young stands of *Pinus taeda* (loblolly pine). A 20 m wide dike (a power line right-of-way) dominated by a thick growth of blackberry 1–1/2 to 2 m high bisects the bay (Fig. 1). Mixed with the blackberries are occasional *Salix nigra* (willow), red maple, and *Magnolia virginiana* (sweet bay), and a cleared strip down the middle of the dike supports a variety of introduced annuals.

### 3. Methods

#### 3.1. Trapping

A 4.0 ha grid consisting of 100 stations with 20 m between traps and a border strip was set in an irregular 'I-shaped' pattern. The main beam of the I extended along the 20 m wide *Rubus* thicket bisecting the Bay (Fig. 1). Crossbeams of the I extended in both directions along the north and south edges of the bay from the water line to the drier upland *Rubus* and shrub thickets. This layout was designed to sample all the major micro-habitats from the water's edge to the dry upland.

Live-traps were prebaited with sunflower seeds for two or three days prior to trapping and were then set and checked for three consecutive days at two to three week intervals from November 21, 1989 through March 5, 1990. Captured animals were ear-tagged and toe-clipped for individual identification, and data on species, sex, age, weight, reproductive condition, and trap location were recorded and the animals released. In mid to late January, feral pigs (*Sus scrofa*) uprooted much of the trapping area along the water's edge altering about 25% of the study site. Due to this damage and increasing water levels throughout the study, some traps were moved to new stations located halfway between existing stations along the edge of damaged or flooded areas. One new line (P) was set on 29 January to replace the largely flooded N-line. An additional 72 traps were set in November for exploratory purposes. Animals were caught at 12 of these sites which are shown with permanent sites in Figure 1.

#### 3.2. Vegetation sampling

We recorded the conspicuous plant species within 2 m of each trap station, estimated ground cover in four categories (1–33%, 34–66%, 67–99% and 100%), and took four measurements of vegetation height at each station. Cover and height were measured before and after water levels changed and pig damage occurred.

#### 3.3. Electrophoresis survey

Starting in mid-January, we took a sample of blood from the suborbital capillary bed of each cotton rat. Standard starch-gel electrophoresis was performed on these samples, testing for the four presumptive loci known to be both available in blood and polymorphic in this area (J. Novak, pers comm). These were 6-phosphogluconate dehydrogenase (6-PGD; 2 alleles), phosphoglucomutase (PGM-1; 2 alleles and PGM-2, 3 alleles), and adenylate kinase (AK; 2 alleles). Data were obtained for 32 individuals. A few were bled on more than one occasion to test our scoring consistency.

### 4. Results

#### 4.1. Trapping success

A total of 71 cotton rats, 79 short-tailed shrews (*Blarinabrevicauda*), 10 rice rats (*Oryzomys palustris*), six cotton mice (*Peromyscus gossypinus*), two harvest mice (*Reithrodontomys humilis*), and two pine voles (*Microtus pinetorum*) were captured 285 times (Table 1). The 71 cotton rats were captured 160 times.

#### 4.2. Population size and breeding season

When trapping began in late November, breeding had already ended. Extrapolating backward based on the size of the youngest individuals present, we estimated that the last births occurred in late October with peak numbers present in mid-November. This timing of the cessation of breeding is consistent with earlier studies in the same area (Odum 1955; Wiegert 1972; O'Farrell *et al.* 1977). By the end of the study in March, reproduction had not yet begun although one male had somewhat enlarged testes. Therefore, population density declined gradually over at least 5 months.

Lincoln Index calculation for early December gives a value of 72 cotton rats. Extrapolating this back to mid-November (based on the rate of decline through December), we estimate that about 98

Table 1. Numbers of trap sites, trap-nights, and capture data for six species of small mammals at the Ellenton Bay study site according to eight vegetation types. Trap-night numbers have also been adjusted for severe pig damage to the habitat that occurred halfway through the study. See text for descriptions of the habitat types.

Vegetation type	Sigmodon								Blarina						Others						
	No. trap sites	No. trap-nights	Corrected no. of trap-nights	Adult males	Subadult males	Unknown sex	Adult females	Subadult females	Totals	Catch per 100 trap-nights	Catch per 100 corrected trap-nights	Unknown sex	Males	Females	Totals	Catch per 100 trap-nights	Catch per 100 corrected trap-nights	Oryzomys	Peromyscus	Microtus	Reithrodontomys
1	39	347	221	4	9	0	7	7	27	7.8	12.2	1	2	3	6	1.7	2.7	5	0	0	0
2	24	349	248	3	10	0	4	3	20	5.7	8.1	1	6	6	13	3.7	5.2	0	0	1	1
3	16	244	244	0	0	0	6	0	6	2.5	2.5	0	3	3	6	2.5	2.5	0	0	0	0
4	10	134	134	3	2	0	2	9	16	11.9	11.9	2	5	2	9	6.7	6.7	1	0	0	1
5	8	72	72	1	7	0	3	2	13	18.1	18.1	0	4	2	6	8.3	8.3	0	0	0	0
6	10	160	160	0	0	0	1	5	6	3.7	3.7	0	1	1	2	1.3	1.3	1	2	0	0
7	24	438	438	19	3	0	8	6	36	8.2	8.2	2	14	13	29	6.6	6.6	6	10	0	0
8	11	253	253	19	9	1	1	6	36	14.2	14.2	0	8	6	14	5.5	5.5	0	10	2	0
Totals:	142*	1997	1770	49	40	1	32	38	160			6	43	36	85			13	22	3	2

\* There were 60 additional traps set on or very close to the grid during the Nov. 22–24 trapping period, and these resulting trap-nights have been included in the totals for the appropriate vegetation categories.

cotton rats (24.5/ha) lived on our study site at the beginning of the decline. By mid-March this population had declined to less than 1/ha. These estimates are concordant with the total number of 71 cotton rats caught on the grid during the study.

#### 4.3. Body weights

All 71 cotton rats caught were assigned to adult or subadult categories based on what they would have been at the beginning of the study. Initially, adult males exceeded 87 g in weight and subadults were less than 70 g. Females were assigned to age categories based primarily on whether they were parous or not. Initially, parous females weighed at least 87 g, with the largest nulliparous female being 76 g.

For the entire study, body weights of adult males and females did not differ significantly (t-test):  $\bar{x}$  males = 117.5 ( $\pm$  4.33);  $\bar{x}$  females = 116.2 ( $\pm$  4.54). Weights peaked in early December and then declined until early February (Fig. 2) with the few survivors then increasing in weight. No adult was known to survive into March. Mid to late December

was unusually cold for this region, and adult females lost more weight than did males. During the late December and mid-January trapping periods males were heavier than females (t-tests;  $p = 0.055$ ;  $p = 0.037$  when means for the two samples were normalized). Subadults of both sexes grew slowly but steadily through the winter, with the males showing more rapid growth starting in early February (Fig. 2).

#### 4.4. Survivorship

Although the study population nearly disappeared by the end of the observed decline, the rate of disappearance varied among the four sex/age cohorts (Fig. 3). Since very few dispersal events were detected over this decline, disappearance rates were assumed to be equivalent to mortality rates.

Adults of both sexes showed the same pattern of loss, declining regularly, but with a slightly higher disappearance rate during the coldest period (early December to mid-January). Subadult females showed the highest initial loss rates, with numbers

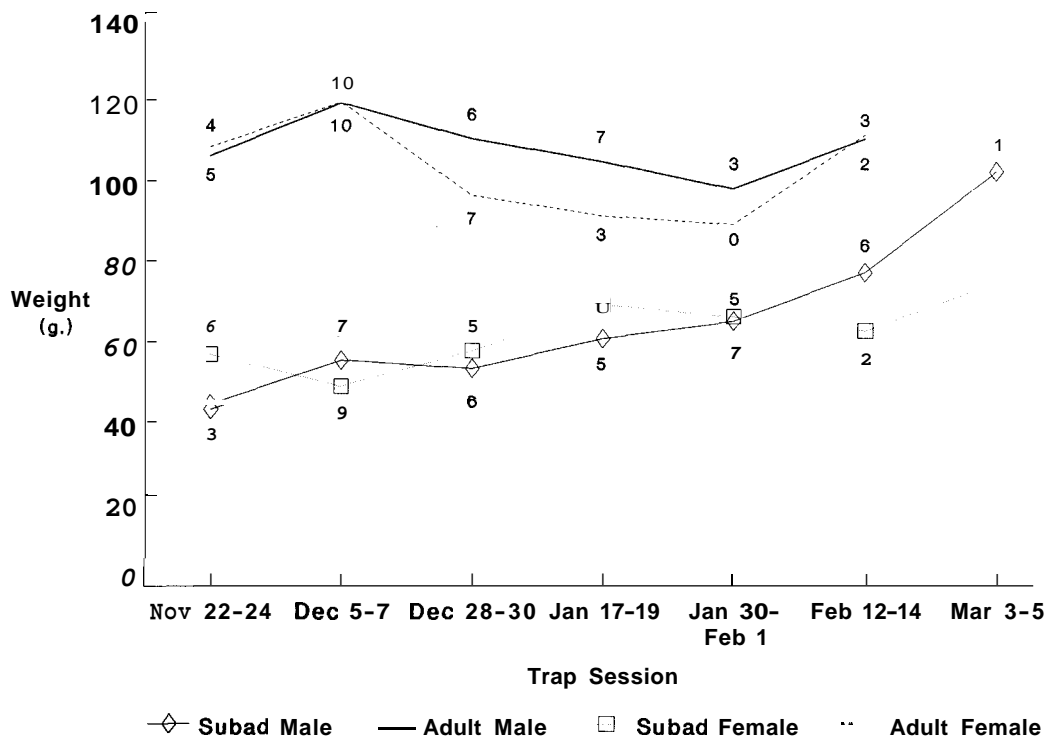


Fig. 2. Average weights of adults and subadults for each sex at each trapping period. Sample sizes are given by each data point. Standard errors are not illustrated because most of the samples are individually too small for these to be meaningful.

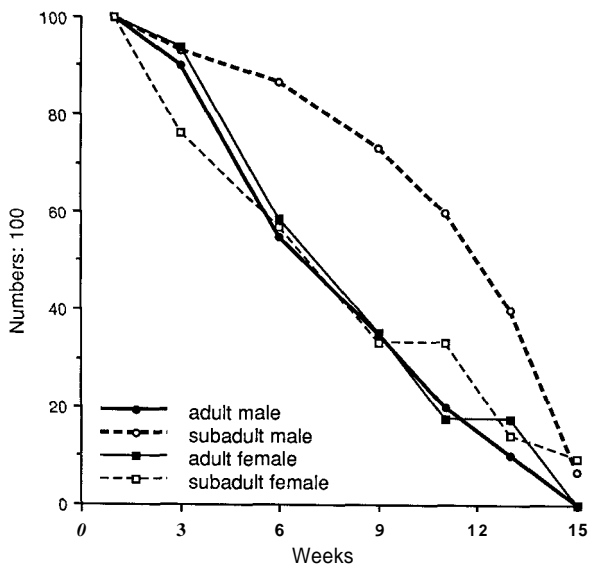


Fig. 3. Survivorship curves for four sex-age cohorts of cotton rats at Ellenton Bay, winter 1989-90 (Nov. 22 to March 5). Losses are based on an initial cohort size of 100 individuals.

declining monotonically from late November to mid-January. After that, they had the highest survival rate of any cohort. Subadult males had the lowest loss rate until the end of January, after which they had the highest. Subadults of both sexes thus ended the decline with equal numbers though they got there by different routes.

#### 4.5. Spatial distribution

Using the results of the vegetation analysis, we assigned each trapsite to one of eight habitat types:

1. *Panicum* grassland at the water's edge;  $\bar{x}$  height = 65 cm.

2. *Andropogon* dominated band just above final water levels;  $\bar{x}$  height = 69 cm.

3. *Panicum* grassland above the *Andropogon*;  $\bar{x}$  height = 47 cm.

4. *Panicum* mixed with low-stature *Rubus*;  $\bar{x}$  height = 47 cm.

5. As in 4, but with significant additional cover

by loblolly pine;  $\bar{x}$  height of herbaceous cover = 52 cm.

6. Open *Panicum*, shrub upland;  $\bar{x}$  height of herbaceous cover = 42 cm.

7. Rubus thicket bounded by open water;  $\bar{x}$  height = 191 cm.

8. Rubus thicket bounded by grassland (mainly *Panicum*);  $\bar{x}$  height = 161 cm.

Habitat-types 1 through 6 were roughly concentrically arranged relative to open water in the bay, except that the altitude gradient on the south and west sides of the bay was steeper so that habitat 3 was absent. An impenetrable tangle of Rubus up to 2–1/2 m tall followed the power line dike, and another patch was located at trapsites M-13 and N-13.

Table 1 shows the distribution of 160 *Sigmodon* captures among these eight habitats. The capture values were also converted into catch per 100 trap-nights to give a better view of habitat use. Trap-nights were further corrected for pig damage since no cotton rats were ever caught in heavily damaged areas. It was apparent that only the drier habitats (3 and 6) were avoided by this species. The most heavily utilized micro-habitats were 5 and 8, which had the tallest and densest cover. Next were the thick, moist *Panicum* grasslands (1), and mixed *Rubus* and *Panicum* (4). Thick *Rubus* patches adjacent to open water (7) were much less used than those next to grassland (8).

Table 1 gives the capture data for the other five species of small mammals caught on our study area. Short-tailed shrews were more uniformly distributed than cotton rats, but avoided the driest (6) and wettest (1) sites. They preferred the same high-cover areas as cotton rats, but utilized the *Rubus* sites next to water (7) much more than did *Sigmodon*. Rice rats were found in sites near open water, although two individuals (1 adult male and 1 subadult female, possibly dispersers) were taken in dry sites. Cotton mice had large home ranges concentrated in the thick *Rubus* (7 and 8). Too few pine voles or harvest mice were caught to draw any conclusions about their habitat preferences.

Looking more closely at the distribution of cotton rats with respect to sex and age groups (Table 1), subadult females were the most generally dis-

tributed subgroup living throughout the grid in all habitat-types except type 3. Subadult males were also generally distributed but with all but four concentrated in two areas, one in the northwest section of the grid and the other in the southeastern corner (Fig. 1). None was captured in either vegetation type 3 or 6.

Adult females were the only sex-age group caught in all eight vegetation types but, with a few short-term exceptions along the *Rubus*-covered dike, did not overlap adult males (Fig. 1). In contrast, adult males were almost completely restricted to dense *Rubus* thickets (Fig. 1) along the dike and in two other smaller blackberry thickets. A few captures were in grassland adjacent to *Rubus* patches.

To increase sample sizes for statistical analysis, we combined the 8 habitat types into 3 patch-types as follows:

A. *Rubus* dominated heavy cover: habitats 5, 7, 8

B. Relatively wet and dense grasslands: habitats 1, 2

C. Relatively dry and open cover: habitats 3, 4, 6.

Utilization was measured by the proportion of captures of each sex-age group adjusted for corrected trap-nights in each patch-type (Fig. 4). Corrected trap-nights were calculated by subtracting trap-sites in locations heavily damaged by pigs. This gives a better measure of *Sigmodon* utilization of patch-types relative to availability of that type. When utilization was calculated by the uncorrected proportion of captures in each patch-type, the values changed slightly in the direction of type A being used more and type B less.

The four sex-age subgroups did not use the available habitat mosaic in the same way. Adult males were almost restricted to the heavy cover habitats (A). Patch-type B was used extensively by adult females and subadult males. Males were almost absent from patch-type C, while this was most frequently used by subadult females. Using Chi-squared tests, we examined the distributions of actual captures and captures corrected for trap-nights against three null models. Expected catch in each patch-type was calculated on the basis of the proportional distributions of 1) total catch ( $n = 160$ ), 2) corrected trap-nights ( $n = 1770$ ), 3) trap-sites (*i.e.*, an estimate of the area) ( $n = 142$ ). In addi-

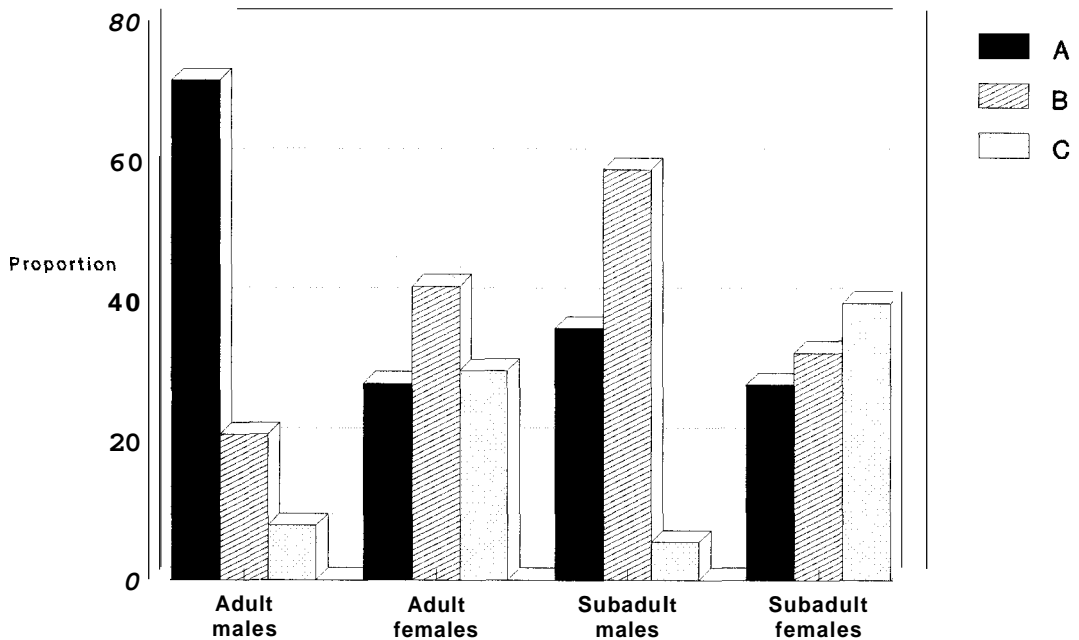


Fig. 4. Habitat use by cotton rats in terms of proportions of catch of each sex-age group per 100 corrected trap-nights in each of three patch types (A, B, and C). See text for description of patch types and definition of corrected trap-night.

tion, by contingency Chi-square, the overall catch in each patch-type was compared with that expected based on distribution of trap sites, and males and females were compared with respect to their distribution in each patch-type.

All three null models gave similar results. The following tests revealed results significantly different from expectations at the  $p < .01$  level for all models: a) overall distribution of four sex and age groups in three patch-types; b) overall distribution of cotton rats in three patch-types; c) males compared with females; d) distribution of adult males in the three patch types; and e) distribution of subadult males in the three patch-types. Subadult females were non-randomly distributed only for the null hypothesis based on overall catch in each patch-type (No. 1), and this was for actual and trap-night corrected catches ( $p = 0.0070$  and  $0.0006$ , respectively). Adult females were randomly distributed in five out of six tests; only with trap-night corrected catches compared to the overall catch did they show a deficiency in their use of patch-type A ( $p = 0.017$ ).

The percent use of patch-type A shifted gradually over the course of the study from 33 to 100%.

Adult male captures were always predominantly in this patch-type. Adult females were initially found primarily in type C but shifted to A and B for the coldest period (Dec. – Jan.), and then completely to A. Subadult males were trapped mostly in patch-type B, but subsequently made increasing use of type A, shifting there completely by early February. Like adult females, subadult females were initially centered in C-patches, but shifted to type B in early December, and thereafter used C and A equally until shifting to A completely by early March.

It seems important to note further that despite the presumably stressful conditions being experienced by this declining population and the large size of our grid, no long-range movements were detected. Four short-distance ( $<80$  m) shifts in home range were recorded by subadults moving into heavy *Rubus* cover.

#### 4.6. Electromorph survey

Of the 71 cotton rats captured, 32 were bled for isozyme analysis (Table 2). PGM-1 was monomorphic in our sample ( $n=30$ ). Both 6-PGD and PGM-2

Table 2. Electrophoretic data for three polymorphic loci;  $n = 32$  cotton rats from Ellenton Bay. Survivors are those 13 individuals known to be present through late February. G tests compare survivors to non-survivors.

Locus <sup>1</sup>	Genotype	Total sample		Survivors		G
		n	%	n	%	
6-PGD	FF	4	12.5	2	15.4	1.86
	FM	9	28.1	2	15.4	
	MM	19	59.4	9	69.2	
PGM-2	AA	19	63.3	7	58.3	1.51
	AC	7	23.3	3	25.0	
	BC	1	3.3	0	0	
	CC	3	10.0	2	16.7	
AK	FF	2	9.1	2	15.4	3.46
	FM	10	45.5	7	53.8	
	MM	10	45.5	4	30.8	

<sup>1</sup> Abbreviations given in text.

were in Hardy-Weinberg equilibrium, but AK had a significant excess of heterozygotes (or a deficiency of the M-homozygotes). Contingency Chi-square comparisons of genotypic frequencies of 13 individuals that survived at least to late February, ('the survivors') with non-survivors gave no statistically significant differences (Table 2). Although sample sizes were small, survivors had a higher frequency of the F-allele at the **AK** locus ( $p = .07$ ).

#### 4.7. Survivors

Of special interest is the group of 13 individuals that survived to near the end of the study (late February): two adult males, three adult females, six subadult males, and two subadult females. Only three subadults were known to have survived into March (Fig. 2). Comparing the survivors by sex and age with the entire sample, no statistically significant differences were found. There was a tendency for adults to be under represented and subadult males to be in excess.

The frequency of the F-allele at the **AK** locus was 31.8% at the beginning of the decline and increased to 42.3% among the survivors. Three out of four known dispersal movements were made by survivors, all four of which were to high density cover.

All 13 of the survivors were located in three sites characterized by heavy *Rubus* cover. In one case, *Rubus* and heavy *Panicum* cover was supplemented by *Pinus taeda* about 3 to 7 m in height.

Finally, we considered the possibility that survivors were able to gain weight through the winter at a different rate than non-survivors. For males, this was not the case as survivors ( $n = 8$ ) gained 1.56 g per week and non-survivors ( $n = 12$ ) 1.55 g. Females gained less than males in general (see Fig. 2), with survivors ( $n = 5$ ) gaining only 0.84 g per week including one adult female who lost 7 g over a 10 week period. Among non-surviving females ( $n = 10$ ), half lost weight and only one, a subadult, gained substantially (17 g in eight weeks). The average for this group was  $-0.67$  g per week.

## 5. Discussion

It is important, although not surprising, to find that a species known to occur in a large variety of habitats does not utilize all habitable patches in the same way and the probability of survival varies greatly among patch-types. Moreover, it is especially significant to discover that the adjacency of two patch-types might be critical to the success of cotton rats. In this study, the juxtaposition of dense cover (*Rubus* thickets) and tall grassland (*Panicum*) seemed to be an attractive habitat attribute. Cotton rats probably utilize these bordering grasslands for foraging.

More surprising is the finding that various sex and age cohorts were distributed dramatically differently with respect to micro-habitat types (Fig. 4). Only adult females were randomly distributed across patch-types, but even they showed temporal shifts in habitat utilization. Adult males occurred in heavy blackberry cover while utilizing adjacent grasslands. Subadult females were dispersed over a wide variety of micro-habitats, but were the heaviest users of the drier grasslands (patch-type C). Subadult males seemed to be semi-colonial, but otherwise used dense cover and wet habitats while avoiding the drier grasslands. All cotton rats surviving to near the end of the study were living in *Rubus* dominated thickets. Moreover, the few doc-

umented dispersal movements occurred into good cover patches. Spencer and Cameron (1983) working on the Texas coastal plain similarly observed that male cotton rats preferred grassy areas with shrub overstory while females showed no preference between two habitats.

In addition to locating in good cover, survivors also had a higher frequency of the F-allele at the adenylate kinase locus. Surviving females gained 1.5 g in body weight per week more than did non-surviving females. Perhaps for females the ability to garner food resources plays an especially critical role in survival sweepstakes. Note that the only two trap deaths occurring in the study were of adult females during an extremely cold period in December. No evidence for negative influences by other species of small mammals was found, as was also reported by Kincaid and Cameron (1985).

The general attraction to dense cover by cotton rats (Fig. 4; Goertz 1964; Kincaid *et al.* 1983; Spencer and Cameron 1983) would seem to implicate predation as being an important factor in their habitat utilization. Numerous mammalian predators occur in the area (Wood and Odum 1965); raccoons (*Procyon lotor*) were particularly evident during our study. The potential for raptor predation pressure is also significant, especially during the winter. Schnell (1968) working in this same area reported significant effects of predation and documented both mammalian and avian predation on cotton rats. He suggested, however, that predator pressure declined drastically as prey population density dropped. Wiegert (1972) also found that predation on cotton rats was a significant factor in their autumn-winter decline, and concluded that avian predators were more important than mammalian.

If predation were singularly critical in causing this population decline, we would expect that adult males which lived most consistently in the best cover would experience the best survival. In fact, adult males survived no better than did the other sex-age cohorts (Fig. 3). Statistically, the sex-age composition of survivors could not be distinguished from that of the initial cohort. However, adults as a whole declined by 88.6% over the study while subadults declined by 75%. Thus other factors

related to age may affect survival rates. Spencer and Cameron (1983) found very similar survival rates between preferred and suboptimal habitats in a population declining over a density range identical to ours (23 to 1/ha).

Our results affirm our initial prediction that a landscape level perspective would allow us to improve our understanding of *Sigmodon* population dynamics. The available habitat mosaic does indeed influence its survival in critical ways. These data also point to the possibility of designing field experiments (*e.g.*, Spencer and Cameron 1983) in which habitat patches of different size, cover features, and juxtapositions can be manipulated to further explore the implications of our findings.

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