HABITAT SEGREGATION IN GROUND CRICKETS: EXPERIMENTAL STUDIES OF ADULT SURVIVAL, REPRODUCTIVE SUCCESS, AND OVIPOSITION PREFERENCE[1]

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Abstract. The closely related ground crickets *Allonemobius allardi* and *A. fasciatus* provide a striking example of habitat segregation. Both species are abundant in pastures and grasslands in the northeastern United States, but they occupy different parts of these habitats. At a site in northwestern Connecticut, we found nearly pure single-species populations at the extremes of a moisture gradient. *Allonemobius allardi* occurred in dry pasture, *A. fasciatus* in wet pasture. Distribution patterns remained constant from one developmental stage to another and from year to year. We undertook a series of experiments to define the factors that determine habitat associations in these crickets. By introducing single-species and mixed-species populations into enclosures in both wet and dry areas, we could demonstrate no significant differences in adult survival or reproductive success between species. Both *A. allardi* and *A. fasciatus* can survive and reproduce in wet and dry habitats. Laboratory choice experiments indicate that differences in oviposition preference also cannot account for field distribution patterns. Indeed, oviposition preference may be a consequence rather than a cause of habitat association.

Key words: adult survival; Allonemobius; crickets; habitat segregation; oviposition preference; reproductive success.

INTRODUCTION

Habitat segregation among closely related or ecologically similar animal species is a common occurrence in nature and may play an important role in resource partitioning and the maintenance of species diversity (Schoener 1974). Factors which may account for such segregation include effects of the physical environment, predation, parasitism, interspecific competition, and innate behavioral differences. In most animal communities the relative importance of these factors for the maintenance of habitat segregation is unknown. Obtaining such information depends, in part, on being able to perform experimental manipulations in the field.

Extensive experimental investigations of habitat segregation among closely related animal species have only been carried out for rodents (e.g., Grant 1969, 1970, 1971, Schroder and Rosenzweig 1975, Glass and Slade 1980, Montgomery 1981) and, to a lesser degree, for sessile invertebrates found along the rocky intertidal (e.g., Connell 1961, Harger 1968, 1970*a, b*, Stimson 1970). The popularity of these groups as objects of experimental investigation is a consequence of both the striking patterns of habitat segregation that they exhibit and the fact that their populations can be manipulated in the field with relative ease.

Equally clear patterns of habitat segregation can be found among groups of insects. However, well-con-

trolled field experiments have rarely been used to distinguish among possible explanations for these patterns. Among the taxa for which habitat segregation has been reported are butterflies (Shapiro and Cardé 1970, Rausher 1979), fruit flies (Fellows and Heed 1972), tenebrionid beetles (Doyen and Tschinkel 1974), spittlebugs (Halkka et al. 1977), leafhoppers (McClure and Price 1976, Stiling 1980), and crickets (Fulton 1931, 1952, 1956, Alexander 1957, Alexander and Thomas 1959, Love and Walker 1979).

The grassland crickets *Allonemobius allardi* and *A. fasciatus* (Grylloptera: Gryllidae) provide a striking example of habitat segregation. Both species are extremely common in pastures of the northeastern United States, but they are found in different parts of such habitats. *Allonemobius fasciatus* inhabits wetter areas, such as low-lying land and land adjacent to ponds and streams. *Allonemobius allardi* occurs in a wider range of habitats but is most common in dry pastures and fields (Fulton 1931, Alexander and Thomas 1959, Paul 1975, Howard 1982). Although mixed populations of the two cricket species occur frequently, it is not unusual for just a few metres to separate nearly pure single-species populations.

Both *Allonemobius allardi* and *A. fasciatus* overwinter in the egg stage and have a single generation each year (Fulton 1931, Alexander and Thomas 1959). In the northeastern United States first-instar nymphs of both species begin to emerge from the soil in early June. Adults can be found from the end of July to the middle of November but reach peak abundance in the 4-wk period from the middle of August to the middle of September (D. J. Howard, *personal observation*).

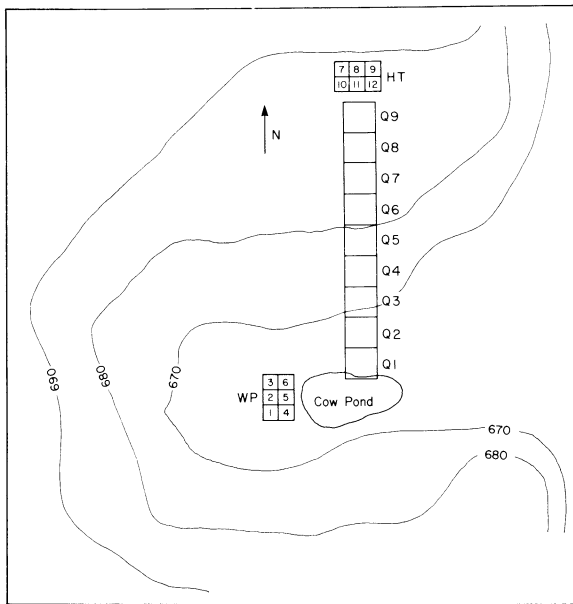[2] Present address: Dept. of Zoology, Michigan State University, East Lansing, Michigan 48824 USA.

FIG. 1.   Map of the study area. Q1–Q9 are 6 × 6 m quad-rats used for sampling species distribution. WP and HT (drawn 2× scale) are enclosures used for transplant experiments.

The two species are extremely similar morphologi-cally. In fact, for many years taxonomists resisted rec-ognizing them as separate species, even though Fulton (1931, 1933, 1937) demonstrated that they could be easily distinguished in the field by song and habitat differences. In 1959, Alexander and Thomas raised these "subspecies" to species status and pointed out morphological characters that could be used to distin-guish pinned adults.

The obvious differences in the distributions of these insects, the tremendous population densities which they often achieve, and their reliance on walking for habitat selection (>99% of adults are short winged and cannot fly) convinced us that they were well suited for ex-perimental investigations of habitat segregation. Three studies are described in this paper. In the first we doc-ument distribution patterns in the field. In the second we analyze survivorship and egg hatch in transplant experiments. In the third we investigate oviposition preference in a laboratory experiment. In a companion paper (Howard and Harrison 1984), we describe an experiment designed to evaluate the significance of habitat selection and interspecific competition as de-terminants of distribution patterns in the field.

MATERIALS AND METHODS

Distribution patterns in the field

We carried out all fieldwork on the Zucker farm at the end of Drum Road in Sharon, Connecticut. The study site was situated in pastures encircling a pond called the Cow Pond (Fig. 1). The Cow Pond covers an area of ≈300 m² and is surrounded to the north,

west, and south by flat or gently ascending land. To the east is a gentle downslope ≈40 m long, which ends at a wooded area. The horseshoe of level ground to the north and south is only ≈20 m wide, before giving way to moderately steep ascending slopes. To the west the ground remains level and very wet for ≈35 m be-fore sloping upward.

We estimated relative species abundances along a transect running north from the Cow Pond. In this direction the horseshoe of level ground abuts a dry, south-facing slope, creating a relatively abrupt tran-sition between wet and dry grassy areas. The transect extended from the edge of the pond to near the top of the south-facing slope and consisted of nine adjacent 6 × 6 m quadrats (Fig. 1). Quadrats 1–3, on level ground adjacent to the pond, represented the wet end of a moisture gradient (although they were not as wet as the area west of the pond). On the slope (quadrats 5–9) the soil was much drier. Quadrat 4 marked the transition between these two areas. Estimates of per-cent cover for plant species along the transect revealed that a variety of grasses (*Festuca elatior, Festuca rub-ra, Poa pratensis, Dactylis glomerata*) occur through-out. The most noticeable change in vegetation from the wet areas to the dry slope was an increase in abun-dance of *Euphorbia cyparissias* and *Galium mollugo*.

On 21 September 1979 we collected 30 adult *Allo-nemobius* from each quadrat, using a sweep net, and identified them to species in the laboratory. Since *A. allardi* and *A. fasciatus* are so similar in morphology and activity patterns, we believe our samples accu-rately reflect the actual species composition, i.e., there is no sampling bias with respect to species. Additional sweep net collections were made on 28 August 1980 and 10 October 1980. At these times virtually all in-dividuals were adults.

To assay distributions of nymphs along the same transect, we used a D-VAC, a gasoline-powered insect vacuum. Collections were made on 13 June 1980, 3 July 1980, and 16 June 1981, when all *Allonemobius* were still early- or middle-instar nymphs. Sixty sec-onds of sweeping with the D-VAC in a given quadrat was usually sufficient to obtain between 25 and 120 nymphs.

We have found no morphological characters that are useful in differentiating nymphs of the two species. However, Howard (1982) has found nearly fixed allelic differences between these species at four loci coding for soluble proteins. We exploited one of these "di-agnostic" loci, malate dehydrogenase (Mdh), to assign nymphs to species. Use of biochemical characters per-mits identification of nymphs for the first time. Field-collected nymphs were transported back to the labo-ratory and stored at −80°C. Using standard techniques of horizontal starch gel electrophoresis (Selander et al. 1971), we assayed individual nymphs to character-ize their Mdh phenotype. We used a pH 6.5 Tris-ci-trate electrode buffer, diluted 1:3 for the gel buffer

(Whitt 1970). Almost no ambiguity exists when identifying nymphs in this manner. Three-banded heterozygotes occur very rarely (<0.2%) and represent either rare hybrids or the occurrence of the allele commonly found in one species as a rare allele in the other.

Transplant studies

We performed transplant experiments with both species to determine whether adult survival and/or ability of eggs to hatch differed between dry and wet pasture. We first staked out two 6 × 6 m areas, one in extremely wet pasture, a few metres from the west bank of the pond (WP), and a second in dry pasture north of and adjacent to quadrat 9, near the top of the south-facing slope (HT). Prior to transplanting adults we made three collections from WP and two collections from HT to document the relative abundance of the two species at these sites (Table 1). Collections from WP always contained >95% *A. fasciatus*. In contrast, *A. fasciatus* was almost never found at HT.

In late July 1980, we built six contiguous enclosures (1½ × 1½ m) at each site (Fig. 1). The 1 m high walls were made of polyethylene, a material that *Allonemobius* cannot climb. We carefully buried all ground edges ≈10 cm. The top of each enclosure was left uncovered, and great care was taken not to damage the vegetation inside.

On 29 July we sprayed each enclosure with Malathion 50 in order to kill all crickets trapped within. This is a relatively safe, effective insecticide. Because adults of both species had first begun to appear only 3–4 d earlier and were still rare in the pastures at this time, we presume that females had deposited few, if any, eggs in the enclosures. The spraying appeared to be very effective. Examination of the enclosures 7 and 13 d later failed to uncover any crickets. However, to ensure that the enclosures were cricket-free we resprayed all enclosures on 21 August.

On 28 August we collected ≈2000 adult *Allonemobius*: 1000 from the south-facing slope (predominantly *A. allardi*) and 1000 from areas adjacent to the Cow Pond (predominantly *A. fasciatus*). Species identifications were made in the laboratory. We then set up four cages each containing 100 *A. allardi*, four cages

TABLE 1. Species composition of collections from hilltop (HT) and west pond (WP) sites.

Sites	Date of collection	Numbers of individuals *A. allardi*	*A. fasciatus*
HT	21 September 1979	30	0
	13 July 1980	66	2
WP	13 June 1980	2	98
	3 July 1980	3	111
	24 July 1980	2	43

TABLE 2. Species composition of adults collected from enclosures on 16 October 1980. Original (4 September) populations were 100 individuals per enclosure (50 + 50 in the mixed-species treatments).

Site	Enclosure number	Original composition	A. allardi Male	Female	Total	A. fasciatus Male	Female	Total
WP	3	*A. allardi*	3	0	3	0	0	0
	4	*A. allardi*	1	9	10	0	0	0
	1	*A. fasciatus*	0	0	0	2	8	10
	6	*A. fasciatus*	2	6	8	4	0	4
	2	mixed	7	3	10	0	6	6
	5	mixed	0	2	2	3	2	5
			13	20	33	9	16	25
HT	7	*A. allardi*	0	4	4	0	0	0
	12	*A. allardi*	5	13	18	0	0	0
	9	*A. fasciatus*	0	0	0	3	6	9
	10	*A. fasciatus*	3	2	5	5	6	11
	8	mixed	7	9	16	3	4	7
	11	mixed	4	2	6	1	3	4
			19	30	49	12	19	31

each containing 100 *A. fasciatus,* and four cages each containing 50 *A. allardi* and 50 *A. fasciatus*. Each cage had equal numbers of males and females of each species. On 4 September, we released one cage of crickets into each of the 12 enclosures. Two replicates of each treatment were represented at both transplant sites (Table 2 and Fig. 1).

We arrived at the numbers to be released as a compromise between the need for adequate sample sizes and a desire not to inflate field densities in the enclosures severely. We estimated field densities of the two species on 24 July 1980 by exhaustively sampling, with D-VAC and net, two 1½ × 1½ m areas, one within 2 m of WP, the other within 2 m of HT. Both collections yielded 34 *Allonemobius*. Thus, release of 100 crickets into an enclosure exaggerated field densities by a factor of three, but was necessary to ensure sufficiently large sample sizes.

Except for weekly checks of the enclosures to look for and repair tears in the walls, we left them undisturbed for the next 6 wk. Only one tear was ever found, in an outer wall of enclosure 10. It was repaired promptly. On 16 October, D. J. Howard spent 7 min in every enclosure catching crickets with a sweep net. Crickets obtained were counted and identified to species in the laboratory.

These collections allowed us (1) to compare adult survivorship within the enclosures and (2) to monitor how effective the enclosures were as barriers to movement of adults. We only censused adults once because more frequent monitoring would have resulted in severe disturbance of the enclosures. Both species of *Allonemobius* tend to hide in the vegetation, and simple visual inspections are not adequate either to count
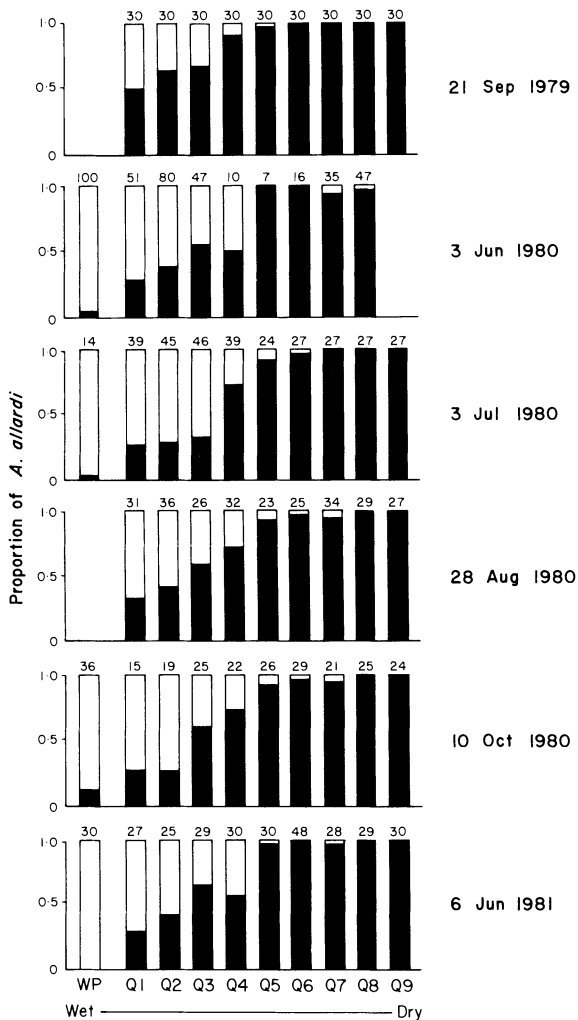
FIG. 2. Proportion of *A. allardi* found in quadrats and at the west pond site over the course of three field seasons. The darkened areas of the bars represent the proportion of *A. allardi*. Number above each bar gives the number of individuals collected.

time to cover the entire area of each enclosure. Nymphs from each enclosure were identified to species by their Mdh phenotype.

Because samples of nymphs from WP contained few individuals, we repeated our enclosure collections on 23 June 1981. On this occasion we collected with the D-VAC for 30 s in all the enclosures at HT but for 2 min in the enclosures at WP. Although we could cover the entire surface area of an enclosure in 30 s, we have found that repeated collection of the same area yields greater numbers of nymphs, i.e., not all nymphs are sucked up the first time around.

For both numbers of surviving adults and numbers of nymphs the following year, we used a three-way analysis of variance with replication (Sokal and Rohlf 1969) to test for effects of species differences, site differences, treatment differences, and interactions between these factors. For analysis we doubled the number of individuals found in mixed-species enclosures to compensate for the initial difference in single-species density. Data were log transformed before analysis. With log-transformed data, doubling values adds a constant value to the effects terms in the analysis of variance but does not change the error distribution.

Oviposition preference

An obvious difference between *A. allardi* habitats and *A. fasciatus* habitats is soil moisture. We wanted to know whether females of either species displayed a strong oviposition preference for dry soil or wet soil and whether this preference might help explain habitat segregation. We investigated this question in the laboratory.

We collected adult females at the Zucker farm on 10 September 1980. On 12 September, 14 females of each species were placed into each of three plastic cages (28 × 29 × 9 cm). Each cage contained four open Petri dishes (90 × 20 mm) filled with 75 mL of a 4:3 sand : soil mixture. The soil in each Petri dish was moistened with 10, 15, 20, or 25 mL of deionized water,

or to identify individuals. We felt that the harmful effects of regularly entering the enclosures and searching for crickets would more than offset the advantages of such a detailed census procedure. We decided to wait until late in the season to sample the enclosures in order to provide females with sufficient time to lay eggs.

Our fences were destroyed during the winter and were rebuilt in April 1981 before any cricket eggs had hatched. In rebuilding, we were careful to lay down the new polyethylene along exactly the same lines occupied by the old polyethylene.

First-instar nymphs of both species begin to appear in this part of North America in early June. We first sampled from the enclosures on 16 June. Using the D-VAC we collected in each enclosure for 30 s, enough

TABLE 3. Three-way analysis of variance with replication, evaluating the effect of species, site, and treatment on survival of adult *Allonemobius*. Before analysis data were log transformed.

Source of variation	df	SS	MS	F_s
Species	1	0.0006	0.0006	0.01 NS
Site	1	0.1269	0.1269	1.27 NS
Treatment (single vs. mixed species)	1	0.1772	0.1772	1.77 NS
Species × site	1	0.0304	0.0304	0.30 NS
Species × treatment	1	0.0242	0.0242	0.24 NS
Site × treatment	1	0.0009	0.0009	0.01 NS
Species × site × treatment	1	0.0328	0.0328	0.33 NS
Error	8	0.8007	0.1001	
Total	15	1.1934		

TABLE 4. Species composition of offspring in enclosures in June 1981. Nymphs were collected on 16 and 23 June. See text for details.

Sites	Enclosure number	Original composition	June composition	
			A. allardi	A. fasciatus
WP	3	A. allardi	12	3
	4	A. allardi	24	1
	1	A. fasciatus	5	35
	6	A. fasciatus	9	28
	2	mixed	7	10
	5	mixed	9	18
			66	95
HT	7	A. allardi	64	1
	12	A. allardi	127	4
	9	A. fasciatus	10	111
	10	A. fasciatus	7	32
	8	mixed	68	91
	11	mixed	36	13
			312	252

giving a range from barely moist to very wet. Position in the cage at one of the four corners was determined randomly. The experiment ran for 4 d, and we randomly changed Petri dish positions within a cage every day. Food (Purina Cat Chow[R]) was evenly scattered throughout each cage, and a wet cotton ball was placed in the center. At the end of the experiment we counted the eggs in each dish.

RESULTS
Distribution patterns in the field

The results of the six collections from quadrats 1–9 are presented in Fig. 2. We also include census data from collections directly adjacent to and inside WP.

Three of the collections (21 September 1979, 28 August 1980, and 10 October 1980) were made when the vast majority of crickets in the field were adults. The other three collections were made when no adults were present, and most individuals were early- (13 June 1980, 16 June 1981) or middle- (3 July 1980) instar nymphs. Nymphs and adults clearly had very similar distribution patterns in the field. Moreover, these patterns were stable during the three years of our study.

WP was the wettest area of pasture and consistently had the highest proportion of A. fasciatus. Along the transect, quadrats 1–4 (the wetter part of the transect) contained a mix of A. allardi and A. fasciatus, with the latter decreasing in abundance away from the pond. Allonemobius fasciatus was only rarely collected on the dry south-facing slope in quadrats 5–9.

Transplant studies

There were no significant differences in adult survival among sites, between species, or between treatments (Tables 2 and 3). Moreover, none of these factors interacts significantly with any other. The number

of adults surviving in each enclosure was only a small fraction of those initially introduced. This was not unexpected, since we delayed our census until mid-October, by which time field populations of A. allardi and A. fasciatus had been declining for a month. Table 2 also shows that for both species we found more females than males.

We found evidence of contamination in two enclosures, numbers 6 and 10. Only A. fasciatus was released into both enclosures, but 5 out of 16 crickets in enclosure 10 were A. allardi, and 8 out of 12 crickets in enclosure 6 were A. allardi. We presume that the A. allardi in enclosure 10 came from adjacent areas of dry pasture where A. allardi is abundant. These crickets may well have entered the enclosure through the hole we found in the polyethylene fence (see Materials and Methods). However, the 8 A. allardi in enclosure 6 were likely the result of leakage from neighboring enclosures, since in this case the contaminating species is rare outside the enclosures. In performing our data analysis we ignored contamination. If the A. allardi in enclosure 6 did come from neighboring enclosures, then our comparisons underestimate the overall survival of that species at WP.

We found no significant differences in the number of offspring produced by the two Allonemobius species at either transplant site (Tables 4 and 5). Moreover, the presence or absence of one species had no significant effect on the number of nymphs produced by the second species. However, site differences did have a significant impact on the number of offspring produced. We found significantly more nymphs of both species in dry pasture (HT) than in wet pasture (WP) ($P < .01$). The significance of this difference is underscored by the fact that we collected for longer periods of time in the WP enclosures than in the HT enclosures.

TABLE 5. Three-way analysis of variance with replication evaluating the effects of species, site, and treatment on Allonemobius offspring production. Before analysis data were log transformed.

Source of variation	df	ss	MS	F_s	Significance (P)
Species	1	0.0061	0.0061	0.07	NS
Site	1	1.2194	1.2194	14.47	<.01
Treatment (single vs. mixed species)	1	0.0000	0.0000	0.00	NS
Species × site	1	0.1729	0.1729	2.05	NS
Species × treatment	1	0.0001	0.0001	0.00	NS
Site × treatment	1	0.0099	0.0099	0.12	NS
Species × site × treatment	1	0.0009	0.0009	0.01	NS
Error	8	0.6740	0.0842		
Total	15	2.0831			

TABLE 6. Number of eggs laid in soil moistened with different amounts of water.

Species	Cage	mL of water				Total	Degrees of freedom		χ^2	Signifi-cance (P)
		10	15	20	25					
		Number of eggs laid								
A. allardi	OP1	25	33	85	108	251		3	77.33	<.005
	OP2	30	23	40	101	194		3	78.78	<.005
	OP3	30	38	61	89	218		3	38.62	<.005
							Total	9	194.73	<.005
	Sum	85	94	186	298	663	Pooled	1	178.39	<.005
							Heterogeneity	8	16.34	<.05
A. fasciatus	OP4	27	37	24	41	129		3	6.04	NS
	OP5	34	42	34	0	110		3	37.82	<.005
	OP6	8	12	9	4	33		3	3.96	NS
							Total	9	47.82	<.005
	Sum	69	91	67	45	272	Pooled	1	15.59	<.005
							Heterogeneity	8	32.23	<.005

Our polyethylene fences clearly did not prevent all movements of nymphs between enclosures, or from outside, as evidenced by contamination of single-species enclosures. Again we ignored contamination in the data analysis. The effect of doing this can be evaluated as follows. We can consider each set of six contiguous enclosures as a single large enclosure into which we introduced equal numbers of the two species. The totals in Table 4 reflect production of offspring in these two large enclosures. Because of the relative species abundances outside the enclosures, any contamination at WP (where A. fasciatus produced more offspring) must have been due to A. fasciatus, and any contamination at HT (where A. allardi produced more offspring) must have been due to A. allardi. At each site contamination from outside could only enhance the apparent success of the species commonly found at that site. Therefore the totals in Table 4 represent a maximum estimate of species differences.

Oviposition preference

Although A. allardi females laid eggs in all oviposition dishes, they clearly preferred the wetter dishes (Table 6). In all three replicates there is a highly significant deviation from random with the most favored oviposition site being the 25-mL water dish (chi-square, $P < .005$). A. fasciatus females do not show the same preference. In two of the three replicates, there is no significant deviation from random. In the third, females entirely avoided the very wet oviposition dish. Overall, A. fasciatus females deposited significantly more eggs in the dish with 15 mL of water (pooled chi-square, $P < .005$). However, the heterogeneity among the replicates makes it difficult to attach much weight to this result. The safest conclusion from these data is that A. fasciatus females exhibit no strong oviposition preference with regard to soil moisture content.

DISCUSSION

The estimates of relative species abundance for 1979, 1980, and 1981 clearly document the habitat association of A. allardi with dry pasture and A. fasciatus with wet pasture. The degree to which the two species are segregated is best demonstrated by comparing the species composition of collections from WP, the wet-test site studied, and collections from HT, one of the driest sites studied. These sites are only 70 m apart in a continuous area of grazed pasture. Of 259 crickets collected during the summer of 1980 from WP, all but 7 were A. fasciatus. Of 98 crickets collected at HT in 1979 and 1980, all but 2 were A. allardi (Table 1). The transect collections also revealed dramatic changes in relative species abundance over a distance of 10–20 m. Moreover, the location of this transition remained constant from one developmental stage to another and from year to year.

What determines the habitat associations of these remarkably similar cricket species? In many groups of insects, habitat association may be a consequence of specific resource requirements, especially dependence on particular food plants. However, different food plant preferences are not an obvious explanation for habitat segregation among ground-living crickets, which probably utilize a wide variety of food resources (Alexander 1968, Harrison 1978).

Differential survival in different habitats could be responsible for observed patterns of habitat association. Differential survival has been implicated in shaping zonation patterns in the rocky intertidal (Connell 1972, 1974). The intertidal is a clearly defined environmental gradient, and transplant experiments can be used to study survivorship in different parts of the gradient. Such direct field experiments have been rare in studies of terrestrial animals, although laboratory studies examining the importance of physiological ad-

aptation have been quite common (e.g., Heller and Gates 1971, Heller and Poulson 1972, Hoover et al. 1977). In our transplant experiments we monitored (1) the number of adults of *A. allardi* and *A. fasciatus* surviving for 6 wk in enclosures built in wet and dry areas of a pasture and (2) the number of offspring they produced the following summer. We did not follow survivorship of nymphs throughout the summer. We found no significant difference in adult survival between species at the two sites (Tables 2 and 3). Although *A. allardi* rarely ventures into the wet pasture at the west end of the Cow Pond (Table 1), adults are capable of surviving there. Similarly, *A. fasciatus* adults are clearly able to survive in the dry pasture at the top of the south-facing slope, although they are rarely found there. Finally, the presence or absence of one species had no significant effect on the survival of the other. Given the striking pattern of habitat segregation of the two species, only if differences in adult survival are large could they be invoked as an important proximate factor limiting distributions. Clearly, differences in adult survival are not large.

Since there was no significant difference in adult survival, the numbers of nymphs in the enclosures the following spring should reflect fecundity of females and survival of overwintering eggs, developing embryos, and early-instar nymphs. We detected no significant difference between species in number of surviving offspring at either WP or HT (Table 5). Obviously, both *A. allardi* and *A. fasciatus* can reproduce and overwinter successfully in habitats in which they ordinarily do not occur. Thus, differential reproductive success cannot be invoked as a proximate factor determining patterns of habitat segregation in these species, although small differences (masked by heterogeneity among our replicates) may, over evolutionary time, have affected patterns of habitat utilization. Although there was no significant difference between species in offspring production at either site, there was a significant difference between sites. Both *A. allardi* and *A. fasciatus* apparently produced more offspring at HT than at WP (Tables 4 and 5). However, this may have been a sampling artifact. Because the enclosures at WP were covered by dense vegetation, the soil was cooler, and egg hatch may have been significantly delayed. (Nymphs collected in the WP enclosures in late June were virtually all first or second instar, while larger nymphs were common on the warmer, drier slope.) If we had collected later in the summer we may not have found a significant difference in numbers between the two sites.

Another factor which can play a critical role in the habitat segregation of closely related insect species is oviposition preference. This is especially true for groups with relatively immobile juveniles (in which case oviposition choice determines habitat associations of the larvae). For example, Fogleman et al. (1981)

have shown that habitat segregation between two species of *Drosophila* found in the Sonoran desert is largely a function of the oviposition preference of one of the species. In the field, larvae of *Drosophila mettleri* occur almost exclusively in soil soaked with cactus rot juices, whereas larvae of *D. nigrospiracula* are found only in rotting cactus tissue. In the laboratory the larvae of *D. nigrospiracula* cannot survive in soaked soil substrate; however, when *D. mettleri* females are forced to oviposit in rotting cactus tissue, the larvae survive as well as they do in soaked soil (Fogleman et al. 1981). Thus, the habitat segregation of these two species is largely a function of the oviposition preference of *D. mettleri*. Similarly, in a study of three *Aristolochia*-feeding swallowtail butterflies, Rausher (1979) demonstrated that habitat segregation of one species, *Parides montezuma*, from two other species, *Battus philenor* and *B. polydamus*, is largely a consequence of oviposition preference. For all three species larval survival and development are enhanced in shady habitats relative to sunny habitats. However, only *P. montezuma* lays most of its eggs in shady habitats.

Our laboratory studies of oviposition preference do not provide any evidence that it plays an important role in the habitat segregation of *A. allardi* and *A. fasciatus*. *A. allardi,* the dry-pasture cricket, prefers to lay its eggs in wet soil, whereas *A. fasciatus,* the wet-pasture cricket, displays no strong preference for wet or dry soil. We can explain this finding if we assume that ground cricket eggs are particularly susceptible to desiccation in dry areas. If so, there may be strong selection for *A. allardi* females to oviposit in the wettest soil available, because the range of soils they normally encounter includes soils that are often too dry but rarely, if ever, too wet. However, *A. fasciatus* is always near wet soil, so there may be no selection pressure to choose wet soil for oviposition. Thus, oviposition preference may be a consequence rather than a cause of habitat association in these ground crickets. This scenario emphasizes that cues used in choosing oviposition site may be independent of those used in habitat selection.

In a companion paper (Howard and Harrison 1984) we explore whether habitat selection or interspecific competition can explain field distribution patterns. We find good evidence for habitat selection in *A. fasciatus* but no support for the notion that current competition affects distribution patterns.

LITERATURE CITED

Alexander, R. D. 1957. The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). Annals of the Entomological Society of America **50**: 584–602.

———. 1968. Life cycle origins, speciation, and related phenomena in crickets. Quarterly Review of Biology **43**:1–41.

Alexander, R. D., and E. S. Thomas. 1959. Systematic and behavioral studies on the crickets of the *Nemobius fasciatus* group (Orthoptera: Gryllidae: Nemobiinae). Annals of the Entomological Society of America **52**:591–605.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710–723.

———. 1972. Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics **3**:169–192.

———. 1974. Ecology: field experiments in marine ecology. Pages 21–54 *in* R. Mariscal, editor. Experimental marine biology. Academic Press, New York, New York, USA.

Doyen, J. T., and W. F. Tschinkel. 1974. Population size, microgeographic distribution and habitat separation in some tenebrionid beetles (Coleoptera). Annals of the Entomological Society of America **67**:617–626.

Fellows, D. P., and W. B. Heed. 1972. Factors affecting host plant selection in desert-adapted cactophilic *Drosophila*. Ecology **53**:850–858.

Fogleman, J. C., K. R. Hackbarth, and W. B. Heed. 1981. Behavioral differentiation between two species of cactophilic *Drosophila* III. Oviposition site preference. American Naturalist **118**:541–548.

Fulton, B. B. 1931. A study of the genus *Nemobius* (Orthoptera: Gryllidae). Annals of the Entomological Society of America **24**:205–237.

———. 1933. Inheritance of song in hybrids of two subspecies of *Nemobius fasciatus* (Orthoptera). Annals of the Entomological Society of America **26**:368–376.

———. 1937. Experimental crossing of subspecies in *Nemobius fasciatus* (Orthoptera). Annals of the Entomological Society of America **30**:201–207.

———. 1952. Speciation in the field cricket. Evolution **6**:283–295.

———. 1956. The genus *Anaxipha* in the United States (Orthoptera: Gryllidae). Journal of the Elisha Mitchell Scientific Society **72**:222–243.

Glass, G. E., and N. A. Slade. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: evidence for competition. Ecology **61**:358–370.

Grant, P. R. 1969. Experimental studies of competitive interaction in a two-species system. I. *Microtus* and *Clethrionomys* species in enclosures. Canadian Journal of Zoology **47**:1059–1082.

———. 1970. Experimental studies of competitive interaction in a two-species system. II. The behavior of *Microtus, Peromyscus,* and *Clethrionomys* species. Animal Behaviour **18**:411–426.

———. 1971. Experimental studies of competitive interaction in a two-species system. III. *Microtus* and *Peromyscus* species in enclosures. Journal of Animal Ecology **40**:323–350.

Halkka, O., M. Raatikainen, L. Halkka, and T. Raatikainen. 1977. Coexistence of four species of spittle producing Homoptera. Annales Zoologici Fennici **14**:228–231.

Harger, J. R. E. 1968. The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. Veliger **11**:45–49.

———. 1970*a*. The effect of wave impact on some aspects of the biology of sea mussels. Veliger **12**:401–414.

———. 1970*b*. Comparisons among growth characteristics of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. Veliger **13**:44–56.

Harrison, R. G. 1978. Ecological parameters and speciation in field crickets. Pages 145–159 *in* P. F. Brussard, editor. Ecological genetics: the interface. Springer-Verlag, New York, New York, USA.

Heller, H. C., and D. M. Gates. 1971. Altitudinal zonation of chipmunks (*Eutamias*): energy budgets. Ecology **52**:424–433.

Heller, H. C., and T. L. Poulson. 1972. Altitudinal zonation of chipmunks (*Eutamias*): adaptations to aridity and high temperature. American Midland Naturalist **87**:296–313.

Hoover, K. D., W. G. Whitford, and P. Flavill. 1977. Factors influencing the distributions of two species of *Perognathus*. Ecology **58**:877–884.

Howard, D. J. 1982. Speciation and coexistence in a group of closely related ground crickets. Dissertation. Yale University, New Haven, Connecticut, USA.

Howard, D. J., and R. G. Harrison. 1984. Habitat segregation in ground crickets: the role of interspecific competition and habitat selection. Ecology **65**:69–76.

Love, R. E., and T. J. Walker. 1979. Systematics and acoustic behavior of scaly crickets (Orthoptera: Gryllidae: Mogoplistinae) of eastern United States. Transactions of the American Entomological Society **105**:1–66.

McClure, M. S., and P. W. Price. 1976. Ecotope characteristics of coexisting *Erythroneura* leafhoppers (Homoptera: Cicadellidae) on Sycamore. Ecology **57**:928–940.

Montgomery, W. I. 1981. A removal experiment with sympatric populations of *Apodemus sylvaticus* (L.) and *A. flavicollis* (Melchior) (Rodentia: Muridae). Oecologia (Berlin) **51**:123–132.

Paul, R. C. 1975. Reproductive isolation in three sympatric species of ground crickets (genus *Allonemobius*). Dissertation. State University of New York, Stony Brook, New York, USA.

Rausher, M. D. 1979. Larval habitat suitability and oviposition preference in three related butterflies. Ecology **60**: 503–511.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27–39.

Schroder, G. D., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia (Berlin) **19**:9–28.

Selander, R. K., M. H. Smith, S. Y. Yang, W. F. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old field mouse *Peromyscus polionotus*. Studies in Genetics **6**:49–90.

Shapiro, A. M., and R. T. Cardé. 1970. Habitat selection and competition among sibling species of satyrid butterflies. Evolution **24**:48–54.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.

Stiling, P. D. 1980. Competition and coexistence among *Eupteryx* leafhoppers (Hemiptera: Cicadellidae) occurring on stinging nettles (*Urtica dioica*). Journal of Animal Ecology **40**:793–805.

Stimson, J. S. 1970. Territorial behavior in the owl limpet, *Lottia gigantea*. Ecology **51**:113–118.

Whitt, G. S. 1970. Genetic variation in supernatant and mitochondrial malate dehydrogenase isozymes in the teleost *Fundulus heteroclitus*. Experientia **26**:734–736.