EXPERIMENTAL EVIDENCE FOR THE INCLUDED NICHE

Interspecific competition has often been examined under the Lotka-Volterra model, which, when applied to an exploitative competitive system, assumes that two competitors completely overlap in the range of resources they use but can differ in their proportional use of resources composing that range (MacArthur 1972; Schoener 1974*a*). However, competitors do not necessarily use the same range of resources (i.e., some proportional uses equal zero for one species over the range of resources used by the other species); this violates the assumptions of the Lotka-Volterra model (Schoener 1974*a*). Often, one or both competitors can exclusively use some resources (proportional use is greater than zero for one species but zero for the other) while overlapping in the use of other resources (both species have a proportional use greater than zero) (Hutchinson 1957; Miller 1967; Schoener 1974*b*). The existence of exclusive resources for one or both competitors increases the likelihood of competitive coexistence (Schoener 1974*b*), since a competitor's numbers cannot be depressed below the number maintained solely on the exclusive resources. Regardless, ecologists frequently rely on the Lotka-Volterra scenario in interpreting experimental data, even though it may yield misleading interpretations of competition in empirical studies (Ayala 1971).

The presence of exclusive and shared resources in a competitive system produces isoclines distinct from those generated by the Lotka-Volterra model, and these isoclines explain the greater likelihood of competitive coexistence when shared and exclusive resources are present (Schoener 1974*b*). Competitive isoclines depict how the number of individuals of a species at equilibrium changes at different constant numbers for the competitor species. Few empirical studies have described competitive population dynamics for which an exclusive resource is present (Gilpin and Ayala 1973, 1976; Schoener 1974*b*, 1975, 1983; Belovsky 1984, 1986*a*), although many studies have either argued that this occurs (Schoener 1983) or have demonstrated that exclusive resources exist for competitors (e.g., Werner 1977). However, evaluating the importance of exclusive and shared resources in competitive interactions can best be accomplished by measuring competitive isoclines.

Gilpin and Ayala (1973) reconstructed what competitive isoclines would look like for two *Drosophila* species on the basis of experimental measures of their population dynamics. The experiment did not measure the isoclines; rather, the population growth trajectories were fitted to likely competitive functions. Abramsky et al. (1991, 1992) inferred competitive isoclines for two desert rodents in field experiments by holding one species' density constant and measuring the other species' behavioral response (dispersal), but this may not adequately reflect population dynamics (i.e., changes in numbers). Competitive isoclines have been measured in field experiments on two grasshopper species (Orthoptera: Acrididae) by holding one species' numbers constant and examining the population response of its competitor. These measurements indicate that the species compete for food when each has both shared and exclusive sets of resources (Belovsky 1986*a*).

Am. Nat. 1994. Vol. 143, pp. 514–527.

When each competitor can use an exclusive range of resources, the explanation for the species' competitive coexistence seems straightforward. However, if one competitor can use exclusive resources and the other can use only shared resources, the latter species is said to have an included niche (Hutchinson 1957; Miller 1967; Schoener 1974*b*), which can lead to its competitive exclusion (Schoener 1974*b*). The included niche has been inferred to occur in nature but has never been empirically demonstrated.

We examined the potential for an included niche using two species of naturally co-occurring grasshoppers. We suggest that the grasshopper *Ageneotettix deorum* (Scudder, white-whiskered grasshopper) has an included niche with respect to *Melanoplus sanguinipes* (Fabricius, migratory grasshopper) since *A. deorum* feeds almost exclusively on grasses (Pfadt 1989) whereas *M. sanguinipes* is a mixed feeder on both grasses and forbs (Pfadt 1988). This was examined through field experiments at the National Bison Range, Montana (Lake County) to measure competitive isoclines and determine whether the isoclines emerge from foraging behaviors of the two species.

METHODS

Experimental Field Populations

Experimental field populations were established in cages. Cages (0.1 m^2 base and 0.8 m tall) were made of window screen and placed over natural patches of vegetation that were similar in plant abundance and species composition. Similar cages have been used to examine grasshopper population ecology in other studies (Belovsky 1986*a*, 1990, 1992; Ritchie and Tilman 1992; G. E. Belovsky and J. B. Slade, unpublished manuscripts; J. R. Moorehead and A. Joern, personal communication). Common grasses were *Poa pratensis* (Kentucky bluegrass) and *Elymus smithii* (bluestem wheatgrass), and the common forb was *Heterotheca villosa* (hairy goldenaster). The cages were stocked with adults of the two grasshopper species that had been caught with nets in the field, kept in a terrarium, and fed ad lib. a mix of natural plants for 3 d. This ensured that injured individuals were not stocked.

Experimental treatments consisted of different density combinations of the two species, which were randomly assigned to each cage. Each treatment had three replicates, and the sex ratio of individuals stocked for each species in a cage was

1:1 (except when an odd number of individuals was stocked, in which case the extra individual was a female). Grasshoppers were stocked on July 27, 1991. For each density combination (treatment), one species' initial numbers were held constant by daily replacing individuals that had died and the other species' numbers were allowed to decrease with mortality.

From previous experiments (Belovsky 1986*a*, 1990, 1992), we knew that (1) the populations allowed to decline would stabilize at a number within 6–10 d, (2) this number would be maintained for up to 45 d, and (3) when a single species was present in a cage, the stable number obtained was the same provided that initial densities (5–20 individuals per cage) were greater than the stable density. These attributes of the system simplify experimental design:

a) A replacement, rather than an additive, experimental design was used (Underwood 1986; Hairston 1989) given observation 3 above; this provided more information with fewer treatments.

b) Whereas the cages did not change the natural abiotic conditions for the grasshoppers (Belovsky and Slade 1993), they did eliminate the grasshoppers' ability to disperse in response to competition, which could have led to competitive mortality. From a population perspective, mortality and dispersal are indistinguishable since both result in a lower density, and a lower adult density reduces recruitment (egg production) to next year's population. However, in a cage, individuals that might otherwise disperse are forced to remain; this might reduce food resources to a greater extent than if they dispersed, since they continue to consume food until they die. This potential difference between competitive mortality and dispersal seemed unimportant, given observations 1, 2, and 3 above, since greater food reduction should have led to a decrease in the stable number as initial density increased.

c) We believe that these within-generation experiments met the criteria for measuring a competitive isocline for univoltine (i.e., one generation per year) species such as these grasshoppers, given observations 1, 2, and 3 above. Furthermore, the stable density attained within a generation usually produced as many or more hatching nymphs in the next year than were needed to match the stable density from the previous year (G. E. Belovsky and J. B. Slade, unpublished manuscript).

The isocline for *Ageneotettix deorum* was measured with initial densities of 0/10, 2/8, 3/7, 4/6, and 5/5 per cage; the numerators of these terms represent *Melanoplus sanguinipes*'s initial numbers maintained at constant values, and the denominator represents *A. deorum*'s initial numbers, which were allowed to decline to a stable number. The isocline for *M. sanguinipes* was measured with initial densities of 0/10, 2/8, 3/7, 4/6, 5/5, and 8/5 per cage; the numerators of these terms represent *A. deorum*'s initial numbers maintained at constant values, and the denominator represents *M. sanguinipes*'s initial numbers, which were allowed to decline to a stable number. An additional combination of 8/5 was used for measuring *M. sanguinipes*'s isocline, since *M. sanguinipes* was known to be less affected by competition with *A. deorum* than *A. deorum* was by competition with *M. sanguinipes* (J. R. Moorehead, personal communication).

In the treatments, five was the lowest initial number used for the population that was allowed to decline, since pilot studies had indicated that both *A. deorum* and *M. sanguinipes* numbers stabilized at approximately five or fewer individuals per cage in the absence of the other species. Also, by maintaining total initial grasshopper numbers at 10 in all but one treatment, we hoped that observed differences between treatments would be due to species composition affecting interspecific competition, not to differences in total grasshopper density. Finally, initial stocking densities in the cages were similar to nymphal densities observed in early July but were higher than adult densities observed at the time of stocking. Therefore, the initial experimental densities were not unrealistic; however, higher than natural densities are required if one wants to observe population declines to stable densities.

Grasshoppers in the cages were counted daily, and all deaths were recorded. Dead individuals of the species held at a constant population were replaced by individuals captured from the field less than 24 h prior to stocking. This ensured that their nutritional status was similar to that of individuals in the cages. The experiment was terminated on September 1, 1991, at which point vegetation in each cage was clipped, separated between grasses and forbs, dried at 60°C for 48 h, and weighed. The quality of the plants as grasshopper food was assessed by their solubility in HCl and pepsin, which is correlated with the grasshoppers' digestion of the plants (Belovsky 1986*a*; G. E. Belovsky and J. B. Slade, unpublished manuscript).

Three sweep samples (August 1, August 16, and September 2, 1991) of grasshoppers from the field were collected. Sweep samples of grasshoppers in grasslands, like our study site, provide unbiased estimates of proportional abundance (Joern and Pruess 1986). Each sample contained more than 50 grasshoppers that were sorted by species, permitting a comparison of proportional (not absolute) field and experimental abundances. Diet composition (grass vs. forb) by microhistological analysis of crop contents (Ueckert 1968) was determined from 10 *M. sanguinipes* and 10 *A. deorum* individuals from sweep samples.

Feeding Trials

Feeding trials with the two species of grasshoppers were conducted to ascertain each species' feeding behavior. Adults of each species (15 of each sex) were placed individually in 11 jars for 24 h with three blades (55 mm × 1 mm) of *P. pratensis* that were held in a water-filled, 2-dram vial with a cotton plug (total plant area above vial was 135 mm^2). The vial was buried in 2–3 cm of soil covering the bottom of the jar. All jars were kept under similar field conditions. Consumption was measured by comparing the area of the grass blades before and after the experiment. Pilot studies showed that the total area of grass provided was considerably less than either species normally consumed under ad lib. conditions during 24 h and that the grass blades would remain fresh for up to 48 h. This experiment determined the maximum proportion of an average blade of *P. pratensis* that an individual would voluntarily consume.

RESULTS AND DISCUSSION

Plant Abundance and Composition

Initially, plant abundance and composition in the cages were similar because of the nonrandom placement of cages in the field and the inspection of the vegetation within each cage; differences in the vegetation were further controlled for by randomly assigning the treatments to cages. Dry weights of vegetation in cages at the end of the experiment, however, were different in that the forbs were more abundant in treatments for which the grass-feeding *Ageneotettix deorum* was present by itself (t-test: $t = 4.89$, df = 31, $P \geq .0001$). Since initially forbs were relatively rare (< 20% by dry mass), this difference did not greatly affect overall plant biomass differences between treatments (ANOVA: $F = 1.91$, df = 1,31, $P \leq .18$). Finally, at the end of the experiment, plant quality did not differ between treatments (ANOVA with arcsine transformation: $F = 1.50$, df = 1,9, $P \leq .25$, for grasses only, since too few forbs remained). Therefore, we concluded that differences in final grasshopper densities between treatments were not due to differences in plant abundances or quality between cages.

Stable Densities for the Grasshopper Populations

Stable densities (constant numbers) for the grasshopper populations allowed to decrease were obtained in each cage 6–10 d after starting the experiment, and this density was maintained for 14–20 d, at which point the experiment was ended (examples for two cages appear in fig. 1). Densities for *A. deorum* when alone were significantly greater than those for *A. deorum* with *Melanoplus sanguinipes* (one-way ANOVA: $F = 15.28$, df = 1,13, $P \leq .002$). The same effect was observed for *M. sanguinipes* when alone and with *A. deorum* (one-way ANOVA: $F = 51.08$, df = 1,16, $P \leq .001$). Therefore, on the basis of the replacement design and the attributes of this system (see Methods), these species appeared to compete in the cages.

The Isoclines

The isocline for *A. deorum* appeared to be linear, whereas that for *M. sanguinipes* appeared to be nonlinear (fig. 2). A nonlinear isocline that approaches an asymptote is expected when a species has exclusive resources, whereas a linear competitive isocline indicates a species with no exclusive resource (Schoener 1974*b*). A competitive system in which one species exhibits an asymptotic isocline and the other a linear isocline is expected in the case of an included niche (Schoener 1974*b*).

The set of equations defining included niche competition (Schoener 1974*b*) is

$$dN_1/dt = R_1 N_1[I_E/N_1 + I_O/(N_1 + \alpha N_2) - C_1] \quad (1)$$

for the species with exclusive resources and

$$dN_2/dt = R_2 N_2[I_O/(N_2 + \beta N_1) - C_2] \quad (2)$$

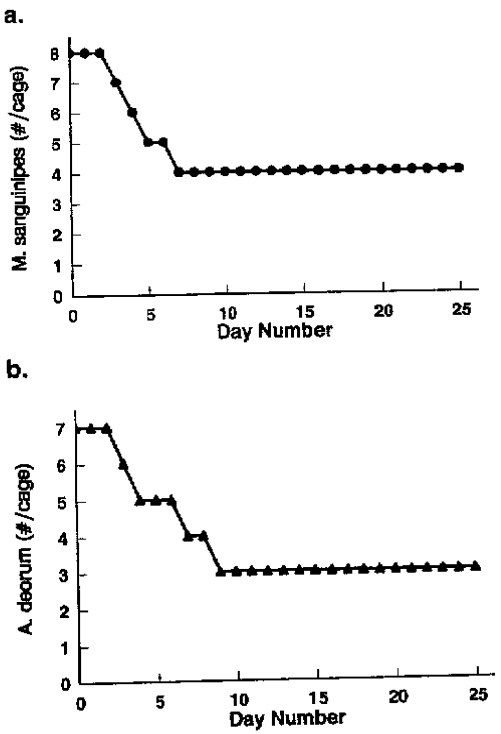

FIG. 1.—Typical census data from two cages, one for *Melanoplus sanguinipes* (*a*) and one for *Ageneotettix deorum* (*b*). The populations declined to a stable density (constant number) within 6–10 d and maintained that density for 14–20 d.

for the species with no exclusive resource. The expression N_i denotes the number of individuals of species i, R_i converts species i's per capita net resource intake into mortality, C_i is species i's per capita resource requirements for maintenance, I_E is the amount of species 1's exclusive resource, I_O is the amount of shared resource available, α converts resource use by species 2 into equivalent use by species 1, and β converts resource use by species 1 into equivalent use by species 2 (i.e., α and β are competition coefficients). The competitive isoclines for this system are

$$N_1 = \{(\alpha C_1 N_2 - I_E - I_O) - [(\alpha C_1 N_2 - I_E - I_O)^2 + 4C_1 I_E \alpha N_2]^{1/2}\}/2C_1 \quad (3)$$

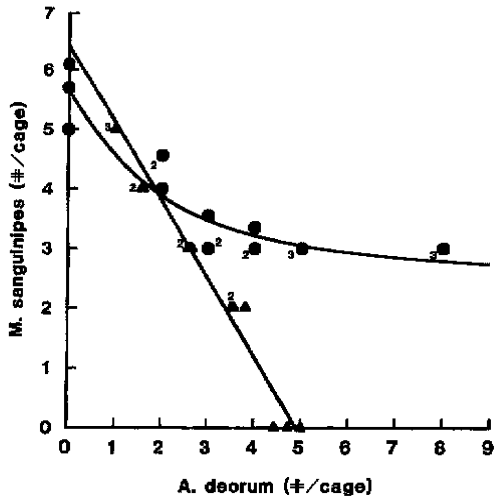

FIG. 2.—The experimental results for grasshopper populations. *Circles* refer to treatments in which *Melanoplus sanguinipes* was allowed to decline to a stable density and *Ageneotettix deorum* density was held constant. *Triangles* refer to treatments in which *A. deorum* was allowed to decline to a stable density and *M. sanguinipes* density was held constant. *Numbers* denote results observed more than once. The *lines* represent the isoclines determined by nonlinear regression analyses that fit hypothesized competition models to the data (see text).

for the species with exclusive resources and

$$N_2 = I_O/C_2 - \beta N_1 \qquad (4)$$

for the species with no exclusive resource.

The isoclines (eqq. [3] and [4]) were fitted to the experimental data according to maximum likelihood nonlinear regression methods available in the statistical package SYSTAT (Wilkinson 1990). For equation (3), N_1 was the stable number for the species allowed to decline and N_2 was the number for the species held constant, whereas the opposite was true for equation (4). The results suggest that *A. deorum* had no exclusive resources, since the linear model (eq. [4]) provided a very good fit to its experimental populations that were allowed to decline (table 1). Fitting the nonlinear model (eq. [3]) to the *A. deorum* data explained an additional 1% of the variance, an insignificant improvement, and provided a very small estimate for *A. deorum*'s exclusive resources ($I_E < 0.001$) that was not different from zero. *Melanoplus sanguinipes* may have both exclusive and shared resources since the nonlinear model (eq. [3]) provided the best fit (table 1).

TABLE 1

SUMMARY OF REGRESSION ANALYSES FOR THE COMPETITIVE ISOCLINES OF TWO GRASSHOPPER SPECIES

	N	df	r^2	*P* Value
Ageneotettix deorum:				
Linear model	15	13	.97	.0001
Melanoplus sanguinipes:				
Linear model	18	16	.62	.0001
Nonlinear model	18	13	.99	.0001

TABLE 2

POPULATION PARAMETERS ESTIMATED FROM THE NONLINEAR REGRESSION ANALYSES OF THE GRASSHOPPER EXPERIMENTAL POPULATIONS

	I/C	I_O/C	Competition Coefficient
Ageneotettix deorum	4.9	4.9	.76
Melanoplus sanguinipes	5.7	3.4	2.26

NOTE.—A number of important population parameters can be estimated from the nonlinear regression analysis of the grasshopper experimental populations by using the variables in the competition equations described in the text. The parameters and their definition in terms of model variables are total carrying capacity ($I/C = I_O/C + I_E/C$), carrying capacity on shared resources (I_O/C), and competition coefficients.

The regression parameters (i.e., slopes, intercepts, and asymptotes) estimated for each population correspond to specific parameters in either equation (3) or equation (4), giving each an ecological definition (i.e., competition coefficients, shared resource abundances, exclusive resource abundances, etc.). If the types of resources being competed for can be identified, the regression parameters (table 2) can be compared with independently obtained estimates of the corresponding ecological values. In previous work (Belovsky 1986*a*, 1990, 1992; Belovsky and Slade 1993; J. R. Moorehead, personal communication), food plants appeared to be the resource competed for at this site. Therefore, laboratory feeding observations on these species can be used to estimate the ecological parameters (competition coefficients and food abundances).

Competition Coefficients

Competition coefficients (α and β) in equations (3) and (4) convert the consumption of a shared food resource by an individual of one species into equivalent consumption by an individual of the other species. An important characteristic of these values is that they are independent of the abundances of the two resources; that is, they represent characteristics of the consumers (fundamental

niche sensu Hutchinson 1957) rather than their consumption in the presence of the competitor species and/or as food abundances change (realized niche sensu Hutchinson 1957).

The competition coefficients in equations (3) and (4) for exploitative competition are defined as the probability that a shared food item when encountered will be consumed by an individual of the other species relative to the probability that it will be consumed when encountered by an individual of the same species (Belovsky 1984, 1986*a*). This ratio of probabilities is computed, for the effect of species 2 on species 1, as (Belovsky 1984, 1986*a*)

$$\alpha = (R_2/C_1)(P_1/P_2)$$

and, for the effect of species 1 on species 2,

$$\beta = (R_1/C_2)(P_2/P_1),$$

where R_i is the removal (i.e., the amount consumed plus the amount harvested but not consumed) of a shared food item by an individual of species i, C_i is the consumption of a shared resource by species i, and P_i is the probability that a shared food item would be consumed by an individual of species i. Each of the parameter values can be computed from aspects of each species' feeding behavior.

Melanoplus sanguinipes in 1991 consumed only 53% grass (SD = 35%, N = 10), even though grass constituted 80% of the biomass at this site. However, *M. sanguinipes* in laboratory feeding preference tests were equally likely to consume grasses or forbs (G. E. Belovsky and J. B. Slade, unpublished manuscript), which indicates that this grasshopper is a generalized feeder as suggested by Mulkern et al. (1969). *Ageneotettix deorum* is known to be a grass specialist (Mulkern et al. 1969), which is consistent with its diet in the field being greater than 90% grass at this site (SD = 5%, N = 10) and with feeding preference observations showing that forbs were almost never consumed (G. E. Belovsky and J. B. Slade, unpublished manuscript). The above results illustrate why the fundamental feeding niche of each species (feeding preferences) must be distinguished from its realized niche (observed diet at the site). Consequently, the shared resource appeared to include only grasses and *M. sanguinipes* was equally likely to eat grass or forb when either was encountered in the absence of competition (P_1 = .5), whereas *A. deorum* ate only grass (P_2 = 1).

The above feeding differences reduced competition but were partially offset by *M. sanguinipes* individuals' consuming twice as much food per day as *A. deorum* individuals when food was presented ad lib. (G. E. Belovsky and J. B. Slade, unpublished manuscript). Differential consumption arose because *M. sanguinipes* has greater nutritional requirements due to its larger body mass (*A. deorum:* 194 mg; *M. sanguinipes:* 391 mg; Belovsky et al. 1990) and the differential consumption provides relative estimates for C_1 = 2 and C_2 = 1.

However, the relative consumption values were modified further by different feeding behaviors observed in our feeding trials. *Melanoplus sanguinipes* fed on a blade of grass by consuming it from the tip downward (30 of 30 trials). In most cases (28 of 30 trials), *A. deorum* individuals cut the blade of grass near the base, consuming a portion from the cut towards the tip and leaving the remaining portion uneaten. Because grass blades desiccate within an hour after cutting to such an extent that *M. sanguinipes* will not eat them, *A. deorum*'s behavior removes resources for *M. sanguinipes* even though *A. deorum* does not consume a portion of the grass blade that *M. sanguinipes* would have consumed. The net effect is that *A. deorum*'s harvesting is equivalent to that of *M. sanguinipes* (R_2 = 1, whereas $R_1 = C_1$ = 2).

The result of the above feeding differences is that *A. deorum* has a greater per capita competitive effect on *M. sanguinipes* for shared resources (α = 1/1 × 1/0.5 = 2.0) than *M. sanguinipes* has on *A. deorum* (β = 2/1 × 0.5/1 = 1.0). Predicted α and β values are similar to regression estimates (table 2).

Shared and Exclusive Resources

Abundances of shared (some grasses) and exclusive (forbs and other grasses) resources determine each species' carrying capacity. The availability of each resource category depends on its biomass in the environment and the proportion that the grasshopper finds acceptable for consumption. Grasses constitute approximately 80% of the plant biomass at the study site.

The voluntary proportional use of grass blades by each grasshopper species was determined in feeding trials by providing less grass than the species could consume; the portion of the blades remaining was assumed to be unacceptable. Sexes in each grasshopper species did not differ in the proportion of grass blades that they voluntarily consumed (*M. sanguinipes* t-test: t = 0.079, df = 28, P > .937; *A. deorum* t-test: t = 1.221, df = 28, P > .232), so that data from the sexes were combined for each species. However, *M. sanguinipes* consumed 1.8 times more of a blade of grass than did *A. deorum* (25.2 ± 6.1 mm^2 vs. 14.1 ± 3.0 mm^2; t = 8.93, $P \leq .0001$). We propose that this difference arises because *M. sanguinipes*'s larger body size enables it to consume plant parts of lower nutritional quality than those consumed by *A. deorum* (Belovsky 1986*b*).

With the above information, the relative abundance of exclusive resources for *M. sanguinipes* can be estimated. First, 20% of the plant biomass (forbs) was not used by *A. deorum*. Second, because *M. sanguinipes* voluntarily consumed 1.8 times more of the available grass in the trials than *A. deorum*, this means that 45% of the grass that *M. sanguinipes* found acceptable was found unacceptable by *A. deorum*. Therefore, the relative abundance of exclusive food resources for *M. sanguinipes* should be 56% of its total food ([0.8 × 0.45 + 0.2] × 100%); the regression estimate was 41% (table 2: 2.3/5.7 × 100%).

Relative resource availabilities can be converted into relative carrying capacities by scaling the availabilities by the grasshopper's relative consumption, assuming that consumption is related to food requirements (e.g., C_1/C_2; see above). Because (1) an *A. deorum* individual consumes half as much as an *M. sanguinipes* individual (C_2/C_1 = 1/2), (2) *M. sanguinipes* shares 55% of the grass with *A. deorum*, and (3) grasses constitute 80% of the plant biomass, the grass specialist, *A. deorum*, is expected to have a carrying capacity that is 88% of *M. sanguinipes*'s (80% × 0.55/0.5). The regression analysis indicated a value of 86% (table 2: 100% × 4.9/5.7).

Relative Abundances of Grasshopper Species

Relative abundances of grasshopper species in sweep samples from the field indicated that the two species constituted 80.0% ± 8.1% (± SD, $N = 3$) of all grasshoppers in 1991, with *M. sanguinipes* being most abundant (> 60%). The competitive equilibrium between the two species in the experiment (intersection of the two isoclines, fig. 2) showed that *M. sanguinipes* constituted 68% of the two species, which was not significantly different from the observed values (73.0% ± 7.5%, ± SD, $N = 3$; $t = 0.60$, $df = 2$, $P < .70$ with arcsine transformation).

Even though the experimental treatments excluded predators, the concordance between experimental results and natural relative abundances suggests that predators were not important for these grasshoppers at this site, which has been documented elsewhere (Belovsky et al. 1990; Belovsky and Slade 1993). Although parasitoids (dipteran and nematode) were not excluded from the experiment (but the adult grasshoppers could become parasitized prior to stocking in the cages), parasitoids were not abundant and did not appear to affect these grasshoppers' populations at this site (parasitism < 5%: Belovsky 1991; M. Lietti de Guibert, J. B. Slade, and G. E. Belovsky, unpublished manuscript).

CONCLUSION

On the basis of the experimental results and their agreement with observed relative abundances, competition coefficients, and resource availabilities in the field, the two grasshopper species appear to exploitatively compete for food. This interspecific competition would appear to operate by one species' (*Ageneotettix deorum*) having its food resources completely included in the wider range of food resources used by the other species (*Melanoplus sanguinipes*), that is, by having an included niche. It has also been suggested that competition between these two species occurs at other sites (Mulkern 1980; J. R. Moorehead, personal communication).

Interspecific competition with an included niche has been suggested by field studies (e.g., Miller 1964, 1967, 1968; Cameron 1971; Colwell and Fuentes 1975; Rusterholz 1981; Schaffer et al. 1983; Gilbert 1985; Bennett 1990) but has never been quantitatively demonstrated as it was in our study. The included niche scenario is generally considered to be rare, since the species with the included niche is perceived to be vulnerable to competitive exclusion. However, the grasshopper that has the included niche, *A. deorum*, is very common throughout much of North America and frequently reaches pest densities in the presence of *M. sanguinipes* (Pfadt 1989).

Theory indicates that species with an included niche must be superior competitors on the shared resources to coexist (Hutchinson 1957; Miller 1967; Schoener 1974*b*), which we observed. However, this is not sufficient to ensure coexistence, since the species with exclusive resources might achieve sufficient density solely on exclusive resources to outcompete the included niche species numerically, even when the latter is competitively superior on a per capita basis (Schoener 1974*b*). This was not observed in our study, since *M. sanguinipes*'s carrying capacity, even though greater than *A. deorum*'s, was not so much greater that *M. sanguinipes* was able to exclude *A. deorum* from the shared resource.

Lotka-Volterra competition models do not distinguish between exclusive and shared resources. Therefore, the above numerical effects on competitive outcomes are often ignored by theory based on these models. Empirical studies that estimate competition coefficients, in light of Lotka-Volterra-based theory, as the change in one species' numbers divided by the abundance of the other species' numbers can produce estimates that vary with competitor abundance (frequency-dependent competition coefficient). The conclusion of frequency dependence can be misleading if the competition occurs exploitatively with shared and exclusive resources. With shared and exclusive resources, the competition coefficients are constants; however, *net* competitive effect depends on the competitor's numbers, its competition coefficient on the shared resource, and the abundances of shared and exclusive resources.

ACKNOWLEDGMENTS

D. Branson, G. Hammond, and J. B. Slade provided help with fieldwork. Comments on earlier drafts of this manuscript were provided by J. R. Moorehead, J. B. Slade, E. E. Werner, H. M. Wilbur, and two anonymous reviewers. This work was supported by a grant to G.E.B. from the U.S. Department of Agriculture/Animal-Plant Health Inspection Service–Grasshopper Integrated Pest Management Project (USDA/APHIS-GHIPM) and the Agricultural Experiment Station, Utah State University. We also thank the personnel of the National Bison Range, Montana, for permission to conduct the study.

LITERATURE CITED

Abramsky, Z., M. L. Rosenzweig, and B. Pinshow. 1991. The shape of a gerbil isocline using principles of optimal habitat selection. Ecology 72:329–340.

Abramsky, Z., M. L. Rosenzweig, and A. Zubach. 1992. The shape of a gerbil isocline: an experimental field study. Oikos 63:193–199.

Ayala, F. J. 1971. Competition between species: frequency dependence. Science (Washington, D.C.) 171:820–824.

Belovsky, G. E. 1984. Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. Oecologia (Berlin) 61:150–159.

———. 1986*a*. Generalist herbivore foraging and its role in competitive interactions. American Zoologist 26:51–69.

———. 1986*b*. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia (Berlin) 70:35–52.

———. 1990. Grasshopper competition. Pages 45–50 *in* 1989 annual report, GHIPM Project, USDA/APHIS/PPQ, Boise, Idaho.

———. 1991. Grasshopper competition and predation: biological control options. Pages 37–44 *in* 1990 annual report, GHIPM Project, USDA/APHIS/PPQ, Boise, Idaho.

———. 1992. Alternate population dynamics for grasshoppers: implications for pest control. Pages 37–44 *in* 1991 annual report, GHIPM Project, USDA/APHIS/PPQ, Boise, Idaho.

Belovsky, G. E., and J. B. Slade. 1993. The role of vertebrate and invertebrate predators on a grasshopper community. Oikos (in press).

Belovsky, G. E., J. B. Slade, and B. A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers: an experimental study. Ecology 71:624–634.
Bennett, W. A. 1990. Scale of investigation and the detection of competition: an example from the house sparrow and house finch introductions in North America. American Naturalist 135: 725–747.
Cameron, G. N. 1971. Niche overlap and competition in woodrats. Journal of Mammalogy 52:288–296.
Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics 6:281–310.
Gilbert, J. J. 1985. Competition between rotifers and *Daphnia*. Ecology 66:1943–1950.
Gilpin, M. E., and F. J. Ayala. 1973. Global models of growth and competition. Proceedings of the National Academy of Sciences of the USA 70:3590–3593.
———. 1976. Schoener's model and *Drosophila* competition. Theoretical Population Biology 9:12–14.
Hairston, N. G. 1989. Ecological experiments: purpose, design, and execution. Cambridge University Press, Cambridge.
Hutchinson, G. E. 1957. Concluding remarks. Cold Springs Harbor Symposia on Quantitative Biology 22:415–427.
Joern, A., and K. P. Pruess. 1986. Temporal constancy in grasshopper assemblies (Orthoptera: Acrididae). Ecological Entomology 11:379–385.
MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York.
Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology 45:256–272.
———. 1967. Patterns and process in competition. Advances in Ecological Research 4:1–74.
———. 1968. Conditions of competition between redwings and yellowheaded blackbirds. Journal of Animal Ecology 37:43–62.
Mulkern, G. B. 1980. Population fluctuations and competitive relationships of grasshopper species (Orthoptera: Acrididae). Transactions of the American Entomological Society (Philadelphia) 106:1–41.
Mulkern, G. B., K. P. Pruess, H. Knutson, A. F. Hagen, J. B. Campbell, and J. D. Lambley. 1969. Food habits and preferences of grassland grasshoppers of the north central Great Plains. North Dakota Agricultural Experiment Station Bulletin 481.
Pfadt, R. E. 1988. Migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), species fact sheet. *In* Field guide to common Western grasshoppers. USDA/APHIS, Wyoming Agricultural Experimental Station Bulletin 912, September 1988.
———. 1989. Whitewhiskered grasshopper, *Ageneotettix deorum* (Scudder), species fact sheet. *In* Field guide to common western grasshoppers. USDA/APHIS, Wyoming Agricultural Experimental Station Bulletin 912, September 1989.
Ritchie, M. E., and D. Tilman. 1992. Interspecific competition among grasshoppers and their effect on plant abundance in experimental field environments. Oecologia (Berlin) 89:524–532.
Rusterholz, K. A. 1981. Competition and the structure of an avian foraging guild. American Naturalist 118:173–190.
Schaffer, W. M., D. W. Zeh, S. L. Buchmann, S. Kleinhans, M. V. Schaffer, and J. Antrim. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64:564–577.
Schoener, T. W. 1974*a*. Some methods for calculating competition coefficients from resource-utilization spectra. American Naturalist 108:332–340.
———. 1974*b*. Competition and the form of habitat shift. Theoretical Population Biology 6:265–307.
———. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecological Monographs 45:233–258.
———. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.
Ueckert, D. N. 1968. Seasonal dry weight composition in grasshopper diets on Colorado herbland. Annals of the Entomological Society of America 61:1539–1544.
Underwood, T. J. 1986. The analysis of competition by field experiments. Pages 240–268 *in* J. Kikkowa and D. J. Anderson, eds. Community ecology: pattern and process. Blackwell Scientific, London.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. American Naturalist 111:553–578.
Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, Ill.

JONATHAN M. CHASE
GARY E. BELOVSKY
DEPARTMENT OF FISHERIES AND WILDLIFE AND ECOLOGY CENTER
UTAH STATE UNIVERSITY
LOGAN, UT 84322-5210

Submitted August 18, 1992; Revised January 29, 1993; Accepted March 23, 1993

Associate Editor: Henry M. Wilbur