

Field tests of competitive interference for space among temperate-zone rodents

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Within-habitat distributions of common rodent species in two temperate-zone small mammal faunas were analyzed by a series of interaction tests to evaluate the hypothesis that the distribution and abundance of these animals is determined by competitive interference for space. In the Rocky Mountains of Alberta, *Peromyscus maniculatus* and *Clethrionomys gapperi* were independently distributed and there was no consistent relationship between the densities of the two species over a broad range of habitats. At Point Pelee National Park in Ontario, *Peromyscus leucopus* and *Microtus pennsylvanicus* distributions were also independent of one another, and again there was no relationship between the densities of these rodents across habitats. These field tests favour rejection of the hypothesis of competitive interference for space among temperate-zone small mammal species.

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La répartition des espèces communes de rongeurs à l'intérieur de l'habitat a été étudiée, par une série d'expériences d'interactions, chez deux communautés de petits mammifères de la zone tempérée, dans le but d'évaluer l'hypothèse selon laquelle la répartition et l'abondance de ces animaux sont fonction de la compétition pour l'espace. Dans les Montagnes Rocheuses d'Alberta, *Peromyscus maniculatus* et *Clethrionomys gapperi* ont des répartitions indépendantes et il n'y a pas de relation définie entre les densités des deux espèces, et cela dans une grande variété d'habitats. Au parc national de la Pointe Pelée, en Ontario, les répartitions des deux espèces *Peromyscus leucopus* et *Microtus pennsylvanicus* sont indépendantes aussi et il n'y a pas de relation définie entre les densités de ces deux populations dans les habitats du parc. Ces expériences nous portent à rejeter l'hypothèse de l'interférence compétitive en fonction de l'espace chez les espèces de petits mammifères de la zone tempérée.

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Introduction

The belief that interference competition for space is an important proximate factor determining the local distribution and abundance of temperate small mammals is firmly entrenched in the ecological literature (e.g., Brown 1978; Grant 1972, 1978). This hypothesis was first proposed when biogeographic studies showed that on islands and peninsular areas where typical woodland rodents were absent, herbivorous voles normally restricted to grasslands occupied woods as well (Cameron 1964; Clough 1964; Grant 1971a; but see Folinsbee et al. 1973). Additional support for the hypothesis came from field and laboratory experiments (Grant 1969, 1971b) which also pointed to aggressive interference for space as the mechanism of competition (Grant 1970). Still further support has come from island introduction experiments (Crowell and Pimm 1976), and from field experiments on other species (Abramsky et al. 1979; Redfield et al. 1977). Competitive interactions remained significant determinants of local distribution even when habitat effects were controlled by multiple regression (Crowell and Pimm 1976; Dueser and Hallett 1980).

In some respects, this emphasis on the importance of interspecific competition is surprising. Several of the species studied are dissimilar in morphology, diet, and behaviour (Brown 1978; but see Master 1977) and are unlikely candidates for competition. Competition among such divergent forms seems to be a contradiction in terms. Is it possible that the interpretation of competitive interference is premature?

Studies of species coexistence have frequently assumed competition and then searched for its effects, rather than evaluating observed distributions against the appropriate null hypothesis of random co-occurrence (Connor and Simberloff 1979; Simberloff and Connor 1981; Strong 1980). A related shortcoming plagues most published studies of temperate rodent assembly. Most lack field confirmation of competitive interference for space. Even mild interference should lead to statistically significant interdependence in the distribution of individuals. Without a decisive test for interaction under field conditions, interpretations of experiments and restricted field observations may be misleading. Manipulation experiments which find interaction can be extended to natural systems only when interaction in the field is confirmed. Similarly, statistical designs which underemphasize the importance of microdistribution

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TABLE 1. Capture frequencies of two common small mammal species caught in each of two replicates of six habitat types in the Kananaskis Valley of Alberta, Canada (51°02' N, 115°01' W)

Species	Habitats											
	Clear-cut		Aspen		Pine		Transition		Spruce		Spruce-fir	
	1	2	1	2	1	2	1	2	1	2	1	2
<i>Clethrionomys gapperi</i>	0	15	6	15	25	30	27	31	25	12	24	35
<i>Peromyscus maniculatus</i>	28	17	0	1	0	4	1	11	26	4	6	29

TABLE 2. Capture frequencies of *Microtus* and *Peromyscus* in four habitats in 1978 and 1979 in Point Pelee National Park in Ontario, Canada (42°00' N, 82°31' W)

Species	Habitats							
	Grassland		Old field		Sumac		Forest	
	78	79	78	79	78	79	78	79
<i>Microtus pennsylvanicus</i>	146	233	39	73	0	0	9	3
<i>Peromyscus leucopus</i>	18	18	18	94	124	326	188	386

can bias the interpretation of species distribution. A casual survey of *Microtus pennsylvanicus* and *Peromyscus leucopus* in eastern North America might suggest local allopatry, yet M'Closkey and Fieldwick (1975) showed that these species co-occur in microhabitats which meet their joint requirements. Any meaningful test for interaction must be of joint distribution within mutually acceptable habitats, otherwise habitat heterogeneity could contribute to apparent species interdependence.

This report details several interaction tests which answer the question: Is the local distribution of co-occurring temperate small mammals consistent with the hypothesis of competitive interference for space?

Methods and statistical design

Small mammals were livetrapped and released in each of two 0.81-ha replicates of six habitats in the Kananaskis Valley of the Rocky Mountains, southern Alberta, and in 2.5-ha plots of four habitats in Point Pelee National Park, southern Ontario (Tables 1 and 2). Single Longworth live traps baited with oatmeal and peanut butter with apple or potato slices for moisture and mattress stuffing for insulation were placed at permanently marked intersections of 15 × 15 m grids. In Alberta, traps were set on alternate trap lines during the evening, checked at first light and midevening the next day,

and then collected at first light on the 2nd day. Each station was monitored in this manner three times from 16 May to 31 August 1977. In Ontario, traps were set along every third line in the evening and collected at first light. Each station, with the exception of a few subject to spring flooding in the forest, was monitored at six more or less monthly intervals from 3 May to 10 November 1978, and at six similar intervals from 16 May to 29 October 1979. In both locations, used and soiled traps were washed with detergent and rinsed with clean water before being moved to another station.

Two by two presence-absence tables tested for interdependence of species' captures at individual stations within habitats. The comparisons presented here deal with *Peromyscus maniculatus* and *Clethrionomys gapperi* in Alberta, and *P. leucopus* and *Microtus pennsylvanicus* in Ontario.

Expected frequencies of *P. maniculatus* and *C. gapperi* occurring with conspecifics or the other species were generated by binomial expansion of the proportions of each species known alive. These expected values were compared with observed results by single classification goodness of fit tests.

Results

Does the within-habitat distribution and abundance of one species of temperate small mammal depend upon the distributional pattern of a second species? An easy test for this competition is to compare stations where

TABLE 3. Presence-absence 2×2 contingency tables of *Peromyscus*-*Clethrionomys* association in three plots in the Kananaskis Valley of Alberta (pooled results for 1977). No expected values are less than 1.0, and Yates correction for continuity applied in all cases

Plot	<i>Clethrionomys</i>	<i>Peromyscus</i>		Total
		Present	Absent	
Clear-cut 2	Present	1	8	9
	Absent	10	30	40
	Total	11	38	49
	$\chi^2 = 0.21$	$p = 0.64$		
Spruce 2	Present	6	9	15
	Absent	7	27	32
	Total	13	36	49
	$\chi^2 = 1.14$	$p = 0.29$		
Spruce-fir 2	Present	8	9	17
	Absent	9	23	32
	Total	17	32	49
	$\chi^2 = 1.02$	$p = 0.31$		

each of the two species were captured and ask: Did they co-occur at individual trap stations more or less frequently than expected by chance alone?

Alberta

The first analysis compared *Peromyscus* and *Clethrionomys* co-occurrence in all habitats with sufficient numbers for analysis. The number of animals known alive was contrasted in each of the first replicates of clear-cut and spruce plots (clear-cut 1 and spruce 1) and the second spruce-fir replicate (spruce-fir 2) for the three 1977 trap sessions combined. In all three cases, *Peromyscus* and *Clethrionomys* were independently distributed (Table 3). This result could mean that *Peromyscus* and *Clethrionomys* did not interact, or that temporal differences in the location of individuals masked competitive effects. This would not be a problem of presence-absence analyses within plots and trap sessions. Such analyses were possible in spruce 1 and spruce-fir 2 during the second trap session, and in clear-cut 1 and spruce-fir 2 during trap session three. In all four analyses, *Peromyscus* and *Clethrionomys* were independently distributed ($\chi^2 < 0.34$; $p > 0.56$).

One problem with 2×2 presence-absence data is that the interaction between rare species may be difficult to assess when a large number of trap stations record neither. Such tables are dominated by the absence-absence cell. This was a problem with *P. maniculatus* and *C. gapperi* in Alberta. Expected frequencies of

conspecific and two species co-occurrence were estimated by binomial expansion of the proportions of *Peromyscus* and *Clethrionomys* known alive. These proportions were estimated by summing the numbers of different individuals known alive in habitats where both species were common (clear-cut 2, pine 2, transition 2, spruce 1, spruce 2, spruce-fir 1 and spruce-fir 2). Observed values were determined by recording the relative numbers of different individuals of *P. maniculatus* occurring at the same trap station, or with *C. gapperi* within study plots and trap sessions. *C. gapperi* co-occurrence was determined similarly. Consequently, co-occurrence in this analysis refers to two or more different individuals being captured at the same trap station within a 36-h period.

Peromyscus and *Clethrionomys* co-occurred less frequently than expected by chance alone, but these results were only marginally significant ($G = 2.72$, $0.05 < p < 0.1$; Table 4).

The basic assumption of this analysis is that individuals are independently distributed and will encounter other individuals of the same or different species in the relative frequencies of their overall abundance. Ideally these proportions should reflect the relative abundance of each species within the encounter radius of a given individual. One of the best estimators of these abundances is likely to be the overall density of each species in a given area or set of habitats, as long as actual encounters are also pooled across the same habitats.

TABLE 4. Single classification goodness of fit test of *Peromyscus*-*Clethrionomys* association in the Kananaskis Valley of Alberta during 1977. Expected values were generated from binomial expectations of minimum numbers of each species known alive multiplied by the total number of co-occurrence cases (28) ($G = 2.72$ with Yates correction for continuity, $0.05 < p < 0.1$)

Association*	Observed	Expected	% deviation from expectation
<i>C.g.</i> × <i>C.g.</i>	11	10.1	+ 8.9
<i>C.g.</i> × <i>P.m.</i>	10	13.8	-27.5
<i>P.m.</i> × <i>P.m.</i>	7	4.1	+70.7

**C.g.*, *Clethrionomys gapperi*; *P.m.*, *Peromyscus maniculatus*.

Alternatively, expectations and observations should be restricted to a particular habitat type, but in this study, that would have created samples too small for analysis. For mobile organisms, binomial probabilities of encounter based on relative abundances also assume that individuals of each species have comparable areas of activity or home ranges. Otherwise, the farther ranging species should encounter conspecifics more frequently than expected. This influence can be corrected by multiplying expected frequencies times the respective ratios of encounter radii of each species comparison. This would seem to be unnecessary for *Peromyscus* and *Clethrionomys*. Beer (1961) found these species to have similar sized winter home ranges in a forest habitat in Minnesota, and Mihok (1979) reported similar summer home range sizes in forested habitats of the Northwest Territories (compare Mihok's Figs. 3 and 4).

I have estimated encounter distances for each species as the mean maximum distance between capture points for individuals captured five or more times. These measures for 17 *Clethrionomys* averaged 71.4 ± 5.48 m, and seven *Peromyscus* had mean maximum capture distances of 73.4 ± 12.81 m. The variances of these estimates within species were homogeneous ($F_s = 2.25$, $0.2 > p > 0.1$; F test, Sokal and Rohlf 1969, p. 186) and mean maximum capture distances were not significantly different (Table 5).

TABLE 5. Similarity of *Peromyscus* and *Clethrionomys* movements in the Kananaskis Valley of Alberta

Source of variation	d.f.	Mean square	F	P
Between <i>Peromyscus</i> and <i>Clethrionomys</i>	1	0.083	0.027	>0.25
Within species	22	3.046		

NOTE: Movements are maximum distances between capture points for animals captured five or more times.

Is it possible that the scale of inquiry dictates the outcomes of the interaction tests of competition? Perhaps *Peromyscus*-*Clethrionomys* competition is manifested by differential use of large habitat patches rather than interdependent co-occurrence at individual trap stations within patches. If this is the case, there should be an inverse relationship between *Peromyscus* and *Clethrionomys* densities across habitats. Where *Peromyscus* are abundant, *Clethrionomys* numbers should be reduced, and vice versa. This was not the case. There was no consistent relationship between *Peromyscus* and *Clethrionomys* numbers across replicated habitats in the Kananaskis (Spearman's rank correlation $r_s = 0.28$, $p > 0.5$).

Ontario

I tested for interference between *P. leucopus* and *M. pennsylvanicus* by again using 2×2 presence-absence tables at individual capture points, and for each year's data, in the grassland and old field in which the two species co-occurred. All four comparisons were non-significant (Table 6). *Peromyscus leucopus* and *M. pennsylvanicus* distributions were independent of one another.

I also tested for reciprocal abundances of the Ontario rodents across habitats. Again, there was no significant relationship between *P. leucopus* and *M. pennsylvanicus* density in the four different habitats in Point Pelee ($r_s = -0.8$, $p > 0.2$ for each of 1978 and 1979).

Discussion

Field evidence against the hypothesis of competitive interference was overwhelming. Only binomial expectations revealed some sort of trend in *Peromyscus* and *Clethrionomys* association. Lack of density correlation among habitats and several nonsignificant interaction tests rule out interspecific competition. A more probable scenario is that *Peromyscus*-*Peromyscus* contagion was more responsible for the marginal significance of the binomial frequencies test than was *Peromyscus*-*Clethrionomys* avoidance (71% as compared with 28% difference from expected values, Table 5). This view is bolstered by Mihok's (1979) observation that two or more *Peromyscus maniculatus* were more frequently found together in multiple capture traps than were *Clethrionomys gapperi* (38% versus 23%, respectively). These combined results indicate that future studies of rodents in boreal forest environments may be most rewarding if designed to understand intraspecific interactions.

There was no support whatsoever for competitive interaction between *Peromyscus* and *Microtus* in Ontario. A sceptic could argue that the within-year presence-absence tables of *Peromyscus* and *Microtus* co-occurrence are biased by temporal differences in the

TABLE 6. Presence-absence 2×2 contingency tables of *Peromyscus*-*Microtus* association in two plots in Point Pelee National Park during 1978 and 1979. No expected values were less than 1.0, and Yates correction for continuity applied in all cases

Plot	<i>Microtus</i>	<i>Peromyscus</i>		
		Present	Absent	Total
1978				
Grassland	Present	6	78	84
	Absent	8	43	51
	Total	14	121	135
	$\chi^2 = 1.66$	$p = 0.20$		
Old field	Present	2	29	31
	Absent	13	91	104
	Total	15	120	135
	$\chi^2 = 0.38$	$p = 0.54$		
1979				
Grassland	Present	12	98	110
	Absent	1	24	25
	Total	13	122	135
	$\chi^2 = 0.46$	$p = 0.49$		
Old field	Present	13	31	44
	Absent	39	52	91
	Total	52	83	135
	$\chi^2 = 1.69$	$p = 0.19$		

location of interactions between these species. Significant interactions may occur, the time scale of which is much less than that reflected by my analysis. These criticisms cannot be answered explicitly with this data set because in any given trap session only one animal could be captured at a particular station. Nevertheless, the hypothesis states that interspecific interactions determine local distribution, and therefore spatial interaction should be observable over a 6-month time span. That all four within-habitat presence-absence analyses of *Peromyscus*-*Microtus* interaction were nonsignificant, and that there was no negative correlation between *Peromyscus* and *Microtus* numbers among habitats, is compelling evidence against the importance of competitive interference in determining the local distribution and abundance of this species pair.

How is it that interference can be demonstrated in the laboratory or in the field experiment, and not be demonstrated in free-living co-occurring populations? One explanation is that temperate-zone small mammals are habitat selectors. For example, Pearson (1959) and Wirtz and Pearson (1960) found significant differences in preferred habitats between *Microtus pennsylvanicus*

and *Peromyscus leucopus* and M'Closkey (1975), M'Closkey and Fieldwick (1975), and Morris (1979) showed that the local distribution of these species could be explained by divergent microhabitat preferences. Other microhabitat analyses of different temperate small mammals confirms habitat separation (Dueser and Shugart 1978; Morris 1980; Vickery 1981). With habitat selection, most natural small mammal encounters will be with members of the same species. Species recognition in such a system is unnecessary, and the rule of small mammal interaction may be "behave to all small mammals as though they are conspecifics." The experiment which artificially increases interspecific encounter probabilities in the laboratory, field enclosure, or removal plot will find interaction, but interaction which is an artifact of the experiment and uninterpretable in a natural context.

Field tests of competitive interference form a logical hierarchy. The easiest first test for spatial competitors is an interaction test similar to those reported here. Where species are independently distributed, competition experiments are unwarranted, and multiple regression estimates of competition (Hallet and Pimm 1979) would

at best give redundant results. But where the interaction tests indicate significant negative association between species, multiple regression can be profitably used to suggest the form of future competition experiments (Dueser and Hallett 1980).

Interaction tests have found little evidence of inter-specific competition for space between common rodent species in two different temperate-zone small mammal faunas. Detailed analyses of local distribution and abundance patterns point instead to habitat selection as the molding force of species assembly in these animals. Even so, interspecific competition through evolutionary time could be responsible for the observed habitat selection (Rosenzweig 1974, 1979, 1981). This is improbable for temperate-zone small mammals which are often markedly different in diet, behaviour, and morphology.

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