

## Sexual differences in habitat use by small mammals: evolutionary strategy or reproductive constraint?

Douglas W. Morris

Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, A1B 3X9, Canada

**Summary.** This study examines the hypothesis that intersexual differences in habitat use by small mammals is an adaptive strategy. Specifically, I evaluate the occurrence of sexual differences in habitat by *Peromyscus* and *Microtus*, and test possible adaptive mechanisms which may lead to such differences.

White-footed mice and meadow voles were live-trapped and microhabitat quantified in four habitats. Sexual differences in microhabitat use were found in three of 12 comparisons. These differences may be related to density dependent resource subdivision and habitat heterogeneity, but neither of these can account completely for the observed patterns. Sexual differences in habitat do not appear to be an evolutionary strategy maximizing reproductive effort by females, or reducing predation. These sexual differences may reduce intraspecific resource overlap, or may simply reflect reproductive constraints limiting female habitat use to suitable nesting areas.

Sexual dimorphism in resource use is common in certain lizards (eg., Schoener 1967, 1968) and birds (e.g., Selander 1966; Storer 1966; Robins 1971; Hespenheide 1975), but sexual differentiation of resources by mammals is less well documented. One of the best examples to date is apparent sexual discrimination of habitat by the deer mouse (*Peromyscus maniculatus*) in xeric plant communities of the southwestern United States (Bowers and Smith 1979). In xeric communities, soil moisture is directly related to plant biomass and vigour, with the result that plant water potential may serve as an *a priori* estimate of small mammal habitat quality (Bowers and Smith 1979). In heterogeneous habitats, female deer mice inhabited more mesic sites and had smaller home ranges than male mice in xeric locations. In homogeneous habitats, no sexual differences were noted. Bowers and Smith (1979) proposed that sexual differences in habitat are adaptive in *Peromyscus* and that females select higher quality locations in the habitat mosaic. This discrimination is impossible in homogeneous habitats where all sites are of similar quality. Three probable advantages were ecological compensation for asymmetry in reproductive costs between the sexes, reduced predation on nest sites and reduced resource overlap. Differential habitat use by sexes of *Peromyscus* may be an evolutionary strategy maximizing female reproductive effort and juvenile survival.

Sexual habitat discrimination by monomorphic species

also suggests that subtle differences in conspecific resource use may be widespread. Such fine-tuned resource partitioning would reaffirm the importance of resource competition to the structuring of ecological systems.

If the Bowers and Smith hypothesis is correct, sexual differences in habitat should be common among *Peromyscus* living in heterogeneous environments. I tested this prediction for the white-footed mouse (*Peromyscus leucopus*) across a variety of habitat types. To evaluate the generality of the hypothesis, I performed similar tests on microhabitat use by the meadow vole (*Microtus pennsylvanicus*).

### Study areas

White-footed mice and meadow voles were live-trapped and microhabitat structure measured in four adjoining habitats in Point Pelee National Park, Ontario, (42° 00' N, 82° 31' W), a large sandspit protruding into northwestern Lake Erie. The mature forest had a diverse mixture of large trees, primarily hackberry (*Celtis occidentalis*), red cedar (*Juniperus virginiana*), silver maple (*Acer saccharinum*), red oak (*Quercus rubra*) and cottonwood (*Populus deltoides*) with an understory of numerous deciduous saplings, chokecherry (*Prunus virginiana*), riverbank grape (*Vitis riparia*) and Virginia creeper (*Parthenocissus quinquefolia*). Adjacent to the forest was an old field (abandoned approximately eight years) densely covered with goldenrod (*Solidago* spp.), wild strawberries (*Fragaria virginiana*), brambles (*Rubus* sp.) and tufted vetch (*Vicia cracca*). This field was being rapidly colonized by red osier dogwood (*Cornus stolonifera*) and saplings of ash-leaved maple (*Acer negundo*) and cottonwood. Abutting the old field was a sumac stand which also developed from an abandoned field and consisted primarily of staghorn sumac (*Rhus typhina*) and red osier dogwood among which several young red cedar were becoming established. Riverbank grape was common throughout, and brambles were the most abundant shrub. The fourth habitat was a wheat-grass (*Agropyron trachycaulum*) grassland with interspersed patches of poison ivy (*Rhus radicans*), riverbank grape, common and rough horsetail (*Equisetum arvense* and *E. hyemale*), and a few young white pine (*Pinus strobus*). Thick clumps of another introduction, black locust (*Robina pseudoacacia*), were suckering from removed parent trees and a pair of overgrown fencerows protruded part-way into the grassland plot.

The four sites span the range of habitats occupied by white-footed mice in this part of North America. They rep-

resent a near ideal mosaic among which to look for sexual differences in habitat use as a function of habitat heterogeneity.

### Field methods and statistical design

Beginning in April 1978, I established a live-trap grid with 15 m intervals between stations in each of the four habitats. The smallest grid (9 × 15) was in the sumac; that in the old field was slightly larger (9 × 16). Grassland and mature forest grids were of equal size (9 × 17). Ecotones between plots were distinct, even though old fencerows separated the sumac from both grassland and old field. To protect against ecotone effects and to achieve equal sized plots for inter-habitat comparisons, the analyses presented here eliminate the peripheral lines in the forest and grassland, and the fencerow line in the old field. In the analyses which follow, all plots were effectively 9 × 15 grids (135 stations each).

From 3 May to 10 November 1978, and again from 16 May to 29 October 1979, each station was live-trapped at monthly intervals. In order to sample the entire study area, each interval consisted of three trap rotations where traps were set out at dusk on every third line and collected at first light. The subsequent rotation trapped the adjacent line, so that each station was censused once each interval. Except for a few stations in the forest which were submerged by spring floodwaters, all stations were trapped six times during each of 1978 and 1979 (6402 total trap nights). Longworth traps containing mattress stuffing as bedding, and baited with a peanut-butter-flour mixture, oatmeal and a slice of potato, were placed within one m of each station. Soiled traps were washed with detergent and rinsed in clean water before being reset.

All captured mice and voles were individually marked with metal ear tags. Age, sex, reproductive status and body measurements were recorded, and the animals released. Jumping mice (*Zapus hudsonius*) and short-tailed shrews (*Blarina brevicauda*) were also captured, but their habitat use is not analyzed here.

I measured habitat at all stations, selecting variables to reflect microhabitat structure and overall habitat heterogeneity (Table 1). Forest density, biomass and composition (TN, TD, TSD, SIZD, STDEN), profile diversity and vertical density (Morris 1979) (Q1, Q2, SUMQ, DIV, AP1, AP2, VERT, DVERT), the mean of four estimates of accumulated litter (LMAT) and variability of litter depth at a given station (CMAT), as well as measures of shrub density and dispersion (SSDEN, SBDEN, BUSHN) were recorded. All diversity variables were calculated using the inverse of Simpson's index ( $1/\Sigma p_i^2$ ). SIZD was calculated by first classifying trees to the following seven basal area (cm<sup>2</sup>) categories: 0 < SIZ1 < 50, 50 < SIZ2 < 100, 100 < SIZ3 < 200, 200 < SIZ4 < 400, 400 < SIZ5 < 800, 800 < SIZ6 < 1600, 1600 < SIZ7. Appropriate data transformations were undertaken where necessary, and only variables whose within-plot frequency distributions were unimodal and more or less symmetrical were used in subsequent analyses (Table 1).

Vegetation profiles and litter depth were measured during the interval 29 June–4 August 1978. To control for possible successional changes in habitat structure in the grassland and old field, these variables were remeasured in these plots between 11 July and 3 August 1979. Tree and shrub

**Table 1.** Variables used for quantifying microhabitat structure in four habitats in Point Pelee National Park (G = grassland, O = old field, S = sumac, F = forest)

Variable	Description	Habitats
Q1	Amount of vegetation from 0–0.25 m	All
Q2	Amount of vegetation from 0.25–1 m	All
SUMQ	Total vegetation below 1.75 m	All
DIV	Vegetation profile diversity	All
AP1	Arcsin proportion vegetation in 0–0.25 m layer	All
AP2	Arcsin proportion vegetation in 0.25–1 m layer	All
VERT	Vertical vegetation density from 1.75 m	0, S, F
DVERT	Vertical density diversity	ALL
LMAT	Log <sub>10</sub> mat depth	G, O
CMAT	Coefficient of variation of LMAT	All
TN	Square root of tree numbers within 3 m	F
TD	Number of different tree species	F
TSD	Tree species diversity	F
SIZD	Tree size diversity	F
STDEN	Square root of distance to nearest tree	All
SSDEN	Square root of distance to nearest sapling	G, O, F
SBDEN	Square root of distance to nearest shrub	G, O, F
BUSHN	Square root of shrub numbers within 3 m	G, O, F

**Table 2.** Summary of the factor analysis of microhabitat structure at 135 stations in the old field habitat at Point Pelee (1979). Varimax rotation was used to simplify factor interpretation. This data set was the most difficult to interpret in terms of microhabitat relationships. Only factors with eigenvalues greater than 1.0 were retained

Variable	Factor loadings				
	I	II	III	IV	V
Q1	−0.08	0.32	−0.07	−0.02	0.91
Q2	0.59	0.43	0.56	0.12	0.23
SUMQ	0.77	0.43	0.08	0.13	0.41
DIV	0.96	0.17	0.09	0.09	−0.08
AP1	−0.84	−0.15	−0.47	−0.14	0.09
AP2	0.30	0.09	0.94	0.10	0.03
VERT	0.23	0.84	0.31	0.16	0.19
DVERT	0.09	0.78	0.16	0.04	0.07
LMAT	0.11	0.02	0.06	−0.03	0.45
CMAT	−0.11	−0.34	0.14	0.04	−0.08
STDEN	0.12	0.05	−0.03	0.32	−0.09
SSDEN	−0.60	−0.05	−0.07	0.15	−0.12
SBDEN	0.04	0.02	−0.11	−0.76	−0.05
BUSHN	−0.10	0.01	0.09	0.86	0.03
% common variation	35.8	13.9	13.1	8.2	7.5

Factor I = Herb-shrub structure; Factor II = Vertical structure; Factor III = Shrub canopy cover; Factor IV = Shrub abundance; Factor V = Herb-mat cover

measures were accumulated from 25 August to 6 December 1978.

I used stepwise multiple discriminant functions analysis (Wilks method, Klecka 1975) to search for sexual differences in microhabitat use separately in each of the four habitats, and in 1978 and 1979. This gave a total of eight

**Table 3.** Correlation matrix among microhabitat variables in the old field habitat at Point Pelee (1978 data). This data set was the most difficult to interpret in terms of microhabitat relationships

	Q1	Q2	SUMQ	DIV	AP1	AP2	VERT	DVERT	LMAT	CMAT	STDEN	SSDEN	SBDEN	BUSHN
Q1	1													
Q2	0.24	1												
SUMQ	0.44	0.82	1											
DIV	-0.10	0.66	0.80	1										
AP1	0.13	-0.79	-0.73	-0.73	1									
AP2	-0.04	0.76	0.36	0.40	-0.73	1								
VERT	0.40	0.72	0.65	0.40	-0.47	0.47	1							
DVERT	0.31	0.49	0.44	0.24	-0.26	0.26	0.77	1						
LMAT	0.42	0.21	0.26	0.09	-0.08	0.11	0.16	0.07	1					
CMAT	-0.17	-0.15	-0.26	-0.14	0.05	0.08	-0.31	-0.22	-0.03	1				
STDEN	-0.08	0.08	0.09	0.18	-0.14	0.03	0.09	0.10	0.02	0.03	1			
SSDEN	-0.07	-0.44	-0.51	-0.56	0.50	-0.23	-0.18	-0.14	-0.14	0.08	-0.02	1		
SBDEN	-0.01	-0.14	-0.09	-0.02	0.11	-0.17	-0.15	-0.03	0.00	-0.04	-0.18	-0.09	1	
BUSHN	0.03	0.12	0.07	-0.01	-0.08	0.14	0.16	0.04	-0.03	0.06	0.30	0.22	-0.71	1

tests for *P. leucopus* and four for *M. pennsylvanicus*, which was abundant only in the field and grassland. Stepwise models test not only for group differences, but also indicate those variables most responsible for the observed separation.

I used factor analysis (Pa2 method, Kim 1975) to estimate habitat heterogeneity and variation in habitat use between sexes at different times. Varimax rotation revealed consistent patterns in the dependence structure of microhabitat. No more than five independent factors were necessary to account for a minimum of 72% of the common variance among the microhabitat structural variables (Table 2). Correlations between variables loading heavily on different factors were negligible (Table 3). This meant that high scores on factor i had no uniform relationship with scores generated from other factors. Furthermore, the factors were consistent in categorizing key structural elements of microhabitat (Morris 1980). Thus I could obtain a unidimensional estimate of microhabitat structure for a given sampling point by summing factor scores at that station. The variation of this new structural variable represents the heterogeneity of a particular habitat. The theoretical probability density function of this new variable is unknown, and microhabitat width is useful solely as a comparison trait. I chose the coefficient of variation of the summed factor scores as a suitable dimensionless dispersion statistic. When all data points for a given habitat are included in the analysis, the mean of the summed factor scores is zero, and a coefficient of variation cannot be calculated. In these instances the standard deviation of the summed factor scores was used as the appropriate estimate of within-habitat structural variation.

## Results

Statistical differences in microhabitat use between *Peromyscus* sexes occurred in three of the eight comparisons (Table 4). Sexual differences in habitat occurred in the grassland in 1978 (separation on the basis of LMAT, a measure of ground layer biomass), and in the heavily populated sumac. Sexual separation in the sumac was complex in that different discriminating variables were responsible for the separation in the two years. Even so, all significant variables in a sense estimated the degree of "shrubbiness" of the sumac habitat. In the sumac, shrubbiness increased with

**Table 4.** Outcomes of tests of sexual discrimination of microhabitat use by *Peromyscus*. All tests were performed by stepwise multiple discriminant functions analyses within particular habitat types

Habitat		Captures <sup>a</sup>	F-ratio <sup>b</sup>	Significant variables
Forest	1978	101 m 78 f	No separation	
Forest	1979	201 m 184 f	No separation	
Old Field	1978	11 m 7 f	No separation	
Old Field	1979	53 m 41 f	No separation	
Grassland	1978	9 m 9 f	11.38**	LMAT
Grassland	1979	14 m 4 f	No separation	
Sumac	1978	68 m 53 f	5.92*	STDEN
Sumac	1979	175 m 150 f	4.97**	BUSHN, DIV

<sup>a</sup> m = males; f = females

<sup>b</sup> F-ratios are not calculated unless separation is significant

\* 0.01 < P < 0.05

\*\* 0.001 < P < 0.01

**Table 5.** Female-male comparisons of mean scores on the three discriminating variables of *Peromyscus* sexual separation in the sumac habitat (standard deviations in parentheses)

Sex	Variable		
	STDEN	BUSHN	DIV
1978			
Male	3.09 (0.948)	2.27 (0.732)	2.52 (0.417)
Female	2.67 (0.956)	2.21 (0.605)	2.49 (0.389)
1979			
Male	2.91 (0.938)	2.28 (0.751)	2.53 (0.384)
Female	2.91 (0.976)	2.10 (0.669)	2.43 (0.446)

the distance to the nearest tree (STDEN) and with increases in BUSHN and DIV.

In southern Ontario, *P. leucopus* is known to prefer complex shrub-like environments (M'Closkey 1975, 1976). In Point Pelee, M'Closkey (1975) showed that the frequency of use of microhabitat patches was linearly dependent upon "branch angle diversity", his estimate of "shrubbiness".

**Table 6.** Habitat heterogeneity in four habitat types in Point Pelee National Park. Heterogeneity is expressed as the standard deviation of summed factor scores for a given habitat

Habitat	Year	Heterogeneity
Grassland	1978	2.32
Grassland	1979	2.09
Old Field	1978	1.93
Old Field	1979	2.21
Forest	1978	2.11
Sumac	1978	1.97

This correlation was greatest in an abandoned apple orchard, a habitat comparable to sumac in this study. The Bowers and Smith hypothesis predicts that females should on average inhabit higher quality habitats than males, that is, in the sumac, females should occupy microhabitats with greater "shrubbiness" indexes than males. The results show just the opposite (Table 5). Males, and not females, were found in the "shrubbiest" microhabitats. In the grassland, increased values for LMAT represent increasing herbaceous cover and biomass, and decreasing habitat quality for *Peromyscus*. In 1978, LMAT was a significant discriminating variable for species separation with *Peromyscus* scoring significantly lower on LMAT than either *Microtus* or *Blarina* (Morris 1980, 1984). According to the Bowers and Smith hypothesis, male *Peromyscus* should have occurred in areas of higher mean scores for LMAT than females. I found the opposite. Mean LMAT for males was 0.24 (standard deviation = 0.031), and for females was 0.43 (0.171).

There were no sexual differences in microhabitat use by *Microtus*.

The second part of the Bowers and Smith hypothesis states that sexual differences in habitat should occur in habitats above some lower threshold of heterogeneity. In this study, heterogeneity indices for *Peromyscus* habitat use should be greater for the sumac and for the grassland (1978) than for any of the other habitats.

The most heterogeneous habitat was the 1978 grassland (Table 6), the same habitat for which *Peromyscus* sexes were significantly different in litter depth (LMAT). The sumac, where sexual differences occurred in both years, was relatively homogeneous.

The Bowers and Smith model is based on competition between sexes for resources in short supply. Above some lower threshold, resource availability should be negatively related to population density. An increase in intraspecific density should lead to increased variability in microhabitat use. Accordingly, sexual differentiation of microhabitat is expected solely in those habitats where density dependent effects occur.

I tested for density dependence in microhabitat by contrasting coefficients of variation of microhabitat use of all *Peromyscus* or *Microtus* captures in a given month with the minimum number of animals of that species known to be alive during that time interval (Table 7). As predicted, density dependent effects on variation in microhabitat use were observed for *Peromyscus* in the sumac. But significant density dependence did not occur in any other habitat even though *Peromyscus* numbers doubled in the forest in 1979 relative to 1978 and more than tripled in the old field (Table 8). *Microtus* numbers also increased, yet despite this, I found no significant density dependence in microhabitat. Are these results biased by a lack of data on seasonal variation in habitat? I doubt it. The tree and shrub data were essentially invariant during my study (the plants grew but did not move) and plant debris was added to the litter in measurable quantities only in autumn. Vegetation profiles in the forest and sumac were mainly due to woody vegetation. Profiles did change seasonally in the grassland and old field, but were likely strongly related to the observed profile recorded when I estimated plant biomass to be at a maximum.

Could transient animals have biased my interpretations of sexual differences? To eliminate transients from the analysis would appear to be overly conservative. First, any categorization of transients must be arbitrary, and statistical

**Table 7.** Association of variability in microhabitat use (coefficients of variation of summed factor scores: CV) with intraspecific population density (minimum number known alive: MNKA) in Point Pelee National Park. The coefficients are large because species' means are near zero in factor space. Only comparisons with sufficient captures for analysis are listed. Total captures (sample sizes) are in parentheses

Trap session	Comparison							
	<i>Microtus</i> in Grassland		<i>Peromyscus</i> in Sumac		<i>Peromyscus</i> in Forest		<i>Peromyscus</i> in Old Field	
	CV	MNKA	CV	MNKA	CV	MNKA	CV	MNKA
1 (3 May–27 May '78)	242.5	8 (9)	408.5	7 (14)			1 (1)	1 (1)
2 (6 June–23 June '78)	137.3	13 (15)	642.5	15 (35)	1291.8	11 (15)		0 (0)
3 (6 July–2 Aug. '78)	189.1	11 (10)	1196.1	12 (31)	1280.2	31 (46)		0 (0)
4 (18 Aug.–30 Aug. '78)	5386.5	22 (23)	788.5	12 (14)	1593.0	27 (45)		0 (0)
5 (16 Sept.–29 Sept. '78)	1393.5	29 (35)	432.9	11 (18)	6012.5	27 (40)		2 (3)
6 (25 Oct.–10 Nov. '78)	1002.0	43 (50)	1043.0	10 (12)	331.9	28 (41)	309.2	9 (14)
7 (16 May–7 June '79)	218.9	21 (21)	726.3	22 (38)	1104.9	33 (51)	250.7	11 (15)
8 (14 June–4 July '79)	246.7	32 (27)	4520.5	36 (76)	1427.3	46 (70)	3092.2	12 (13)
9 (17 July–9 Aug. '79)	195.7	44 (36)	2843.1	36 (61)	2739.5	60 (85)	385.0	11 (14)
10 (17 Aug.–31 Aug. '79)	355.5	48 (41)	4119.5	34 (60)	2932.9	51 (73)	2174.1	14 (18)
11 (5 Sept.–20 Sept. '79)	1270.8	59 (63)	3925.5	36 (52)	501.0	45 (54)	652.6	13 (19)
12 (2 Oct.–29 Oct. '79)	2170.3	42 (45)	516.8	28 (39)	510.2	41 (53)	179.7	12 (15)
Kendall's tau	0.24	$p=0.136$	0.50	$p=0.013$	0.04	$p=0.438$	0.35	$p=0.14$

**Table 8.** The number of different individuals of *Microtus* and *Peromyscus* and transient *Peromyscus* captured in four habitats at Point Pelee National Park during 1978 and 1979

Species	Habitat			
	Grassland	Old field	Sumac	Forest
1978				
<i>Microtus</i>	97	26	0	5
<i>Peromyscus</i>	10	11	31	59
Transient <i>Peromyscus</i>	1	1	5	5
Species	Habitat (% change in parentheses)			
	Grassland	Old field	Sumac	Forest
1979				
<i>Microtus</i>	147 (51)	30 (15)	0 (0)	2 (-60)
<i>Peromyscus</i>	11 (10)	39 (254)	84 (171)	121 (105)
Transient <i>Peromyscus</i>	2	6	19	22

transients (adult animals captured once and not again) do not necessarily correspond to biological transients. Some single capture animals, for example, are likely occupying long-term home ranges and are not captured subsequently due either to death or trap shyness. Second, even adult transients may select microhabitats similar to other individuals in their age and sex class.

Eliminating transients from the analysis would seem to be desirable and necessary only if the proportion of transient individuals depended upon habitat or year classifications in the overall data set. I checked for this dependence by evaluating the proportion of transient animals (adults captured once) to the number of different individual *Peromyscus* captured in each habitat in each year (Table 8). The resulting three-way contingency table was analyzed by hierarchical log-linear models (Sokal and Rohlf 1981; pp 747–765), all of which were non-significant. The proportion of transient individuals was independent of habitat and yearly classifications.

There were significantly more male transients (44 males; 15 females) than expected relative to the proportion of males in the population as a whole (201 males; 153 females) (test of binomial proportions, Sokal and Rohlf 1981; p 693;  $P < 0.01$ ). This is interesting in that it indicates less home-site fidelity in males than in females, but it had no impact on the analysis of sexual differences because the proportion of transients was independent of habitat and temporal effects.

## Discussion

Sexual discrimination of microhabitat by *Peromyscus* occurred in three out of eight comparisons, yet in contrast to the Bowers and Smith hypothesis, sexual separation was not consistently related to habitat heterogeneity. A habitat heterogeneity argument is insufficient to account for instances of sexual differences observed at Point Pelee.

This analysis also questions the mechanism responsible for sexual differences in resource use by *Peromyscus*. Bowers and Smith postulated a selective advantage to domi-

nant females which selected optimal locations in the habitat mosaic. Possible selective advantages included increased reproductive effort by females, reduced predation and lowered resource overlap. All three imply intersexual competition because males are displaced to less optimal locations. But at Point Pelee, male *Peromyscus* selected the highest quality microhabitats. Of the three alternative explanations, this result is compatible only with reduced intraspecific resource competition. The importance of intraspecific competition to sexual differences in microhabitat is reinforced by noting that significant intraspecific density dependent effects on microhabitat "width" occurred solely in the sumac. Intersexual differences in microhabitat appear advantageous, but are expressed only in extremely variable habitats (grassland, 1978), or in habitats where intraspecific competition is intense (sumac).

This interpretation is underscored by my observations of infrequent sexual differences in habitat use by *P. leucopus*, and an absence of such differences in microhabitat by *Microtus*. Bendell (1961) also noted significantly different habitat associations of male and female *P. leucopus*. These associations were significant in but three of 23 comparisons. Consistent with my results, all three of the significant sexual differences were caused by a greater number of males in a particular habitat than expected by chance (Bendell 1961).

Sexual dimorphism has been linked to both sexual selection (eg., Trivers 1972) and to differential resource use (Schoener 1965; Selander 1966). A sexual selection hypothesis is unlikely to account for the *Peromyscus leucopus* sex differences because sexual differences related to mating behavior should be adaptive independent of population density, and should occur in all habitats.

Ecological dimorphism should be most common in animals which also show dimorphism in feeding structures or in other obvious ecomorphological and ecophysiological traits. Such characters as intersexual differences in body size for poikilotherms (Schoener 1967, 1974) and trophic structure in homoeotherms (Schoener 1965; Selander 1966) most commonly reflect ecological segregation. Behavioural segregation has previously been associated only with territorial species (Robins 1971; Hespender 1973, 1975; Schoener 1977; Morse 1980). Behavioral resource partitioning could be a consequence of intraspecific competition for resources or could be caused by other adaptive behaviors. Morse (1968) reported sexual differences in foraging by *Dendroica* warblers, but it is not clear whether this is an adaptive behavior partitioning resources between the sexes, or whether it is related to individual economy through male territorial defense and female incubation. Most likely, the adaptive value of the behavioral differences is reinforced by any additional advantage procured from reduced sexual overlap in resource use.

*Peromyscus* appears to be at least somewhat territorial in that females often have mutually exclusive home ranges (Metzgar 1971). Metzgar (1971) also reported that for *P. leucopus*, the degree of exclusiveness of home range increased with population density. This, if true, may be sufficient to account for the apparent density dependent effect on sexual differences in microhabitat in Point Pelee National Park.

The significant sexual separation in the grassland in 1978 supports the Bowers and Smith hypothesis that sexual discrimination should occur in heterogeneous environ-

ments. But the comparison of the grassland separation with that in the sumac points to intraspecific density as the main organizer behind sexual differences. It is unfortunate that Bowers and Smith did not first test for density dependence of microhabitat use prior to formulating their habitat heterogeneity – sexual dimorphism model.

Sexual differences in microhabitat may represent a subtle form of resource partitioning among conspecific small mammals. In the present case, for two out of the three comparisons, sexual differences were linked to evidence of density dependent microhabitat expansion. But the characteristics of individual habitats must also influence strategies of intraspecific resource partitioning because there were no density dependent effects on microhabitat for *Peromyscus* in the forest (a 105% increase in 1979) and for *Microtus* in the grassland (51% increase).

Habitat selection theory (Rosenzweig 1974, 1981) predicts that in patchy environments a coarse-grained strategy (selectivity) is superior to all others. This corresponds to the Bowers-Smith postulate that there is some lower threshold of habitat heterogeneity above which sexual differentiation is possible. The question now becomes, how do we reconcile a low heterogeneity index in the sumac with observed sexual differences in microhabitat? One answer may lie in the mode of social organization and population regulation of *Peromyscus*. In *Peromyscus*, female territoriality may be density dependent (Metzgar 1971). As population density increases, dominant females should exclude subordinates from defended sites. At low density, competition for these sites is reduced and all individuals should be able to locate sites with similar rewards. Female aggression could effectively increase habitat patchiness above the specialization threshold. In territorial species, habitat heterogeneity has both a physical and social component. Unless social organization of Point Pelee *Peromyscus* is fundamentally different from Metzgar's view of density dependent female territoriality, this argument does not seem to explain why males consistently selected higher quality habitats than females. M'Closkey's (1975, 1976) observations and experiments recorded the use of different structural classes of vegetation by free-ranging *Peromyscus*. If we consider these records in the broad context to represent foraging behavior, then we interpret male preference for shrubby microhabitats as habitat selection on the basis of resources. Even if sexual dimorphism in *Peromyscus* is a strategy to reduce resource competition, its mechanism needs reappraisal.

An alternative explanation for *Peromyscus* sexual differences in microhabitat is simply that during the breeding season, females and males have different habitat requirements. Females must select safe nest sites for their young (both predation and physiological components), and must spend considerable time at or near those sites nurturing young. Small female home ranges may be more of a constraint of mammalian reproduction than an adaptation enabling foraging in resource rich habitats. Males also require nest sites, but their negligible parental responsibilities give greater freedom and opportunity to select microhabitats on the basis of resource levels or mate availability.

What seems to be required for sexual dimorphism is not just habitat heterogeneity, but heterogeneity in the dispersion patterns of suitable female nest sites. In the old field, released *Peromyscus* were quickly lost from sight after entering dense clumps of brambles and other vegetation, and in the forest, a variety of arboreal and terrestrial refuges

were used. But in the grassland, *Peromyscus* consistently sought shelter along abandoned fencerows or in clumps of shrubs, and in the sumac, in subterranean burrows. The fencerows represent linear patches in the grassland, and it is likely that heterogeneity in soil characteristics and plant cover dictated heterogeneity in the placement of burrow systems in the sumac. Plant succession reduced habitat heterogeneity in the grassland in 1979, and sexual discrimination of microhabitat did not occur. Nest site availability in the sumac was likely heterogeneous in both years, and the observed sexual differences support that view.

Then why did females select the most optimal microhabitats in Bowers' and Smith's study? One answer is that desert dwelling *P. maniculatus* have a fundamentally different social organization than forest and shrubland *P. leucopus*. But again there is a simpler explanation because there is no reason to propose a consistent negative correlation between nest site availability and resource abundance. In xeric environments in the southwestern United States, for example, moist microhabitats may often be both an indicator of favorable nest sites, and abundant resources. Under these conditions, dominant females selecting suitable nest sites will also select higher quality habitats than males.

Sexual differences in microhabitat use by small mammals appear to be restricted to heterogeneous environments. This may serve to reduce intraspecific competition for resources, but is more likely related to intrinsic differences between the sexes in their habitat requirements.

*Acknowledgments.* I am indebted to Kelly Morris for field and technical assistance, for computer programming, help in data analysis and emotional support. Paul Anderson shared friendship, ideas and concepts freely and with enthusiasm, and provided logistical and administrative assistance. George Cox provided a thorough critique of an earlier version. The suggestions of Alan Whittick and anonymous reviewers improved the paper. Parks Canada endorsed my research and gave me access and logistical support at Point Pelee. John Enright and David Morris helped with live-trapping. Jack Enright helped predator-proof my Longworth traps. Monarch Mattress Company provided nesting material on short notice and free of charge. I received scholarship support from the Natural Sciences and Engineering Research Council of Canada, the Isaac Walton Killam Foundation, the Province of Alberta and the University of Calgary. To all I am most grateful. This work was supported in part by grants from the Natural Sciences and Engineering Research Council of Canada and formed a sub-set of research toward a Ph.D. thesis at the University of Calgary.

## References

- Bendell JF (1961) Some factors affecting the habitat selection of the white-footed mouse. *Can Field-Nat* 75:244–255
- Bowers MA, Smith HD (1979) Differential habitat utilization by sexes of the deer mouse, *Peromyscus maniculatus*. *Ecology* 60:869–875
- Hespenheide HA (1973) Ecological inferences from morphological data. *Ann Rev Ecol Syst* 4:213–229
- Hespenheide HA (1975) Prey characteristics and predator niche width. In: *Ecology and evolution of communities*. Cody ML, Diamond JM (eds) Belknap Press, Cambridge pp 158–180
- Kim J (1975) Factor analysis. In: *Statistical package for the social sciences*, 2nd edition Nie NH, Hull CH, Jenkins JG, Steinbrenner K, Bent DH (eds) McGraw-Hill, New York pp 468–514
- Klecka WR (1975) Discriminant analysis. In: *Statistical package for the social sciences*, 2nd edition Nie NH, Hull CH, Jenkins JG, Steinbrenner K, Bent DH (eds), McGraw-Hill, New York pp 434–467

- M'Closkey RT (1975) Habitat dimensions of white-footed mice, *Peromyscus leucopus*. *Am Mid Nat* 93:158-167
- M'Closkey RT (1976) Use of artificial microhabitats by white-footed mice, *Peromyscus leucopus*. *Am Mid Nat* 96:467-470
- Metzgar LH (1971) Behavioral population regulation in the woodmouse, *Peromyscus leucopus*. *Am Mid Nat* 83:434-447
- Morris DW (1979) Microhabitat utilization and species distribution of sympatric small mammals in southwestern Ontario. *Am Mid Nat* 101:373-384
- Morris DW (1980) The pattern and structure of habitat utilization in temperate small mammals. Ph.D. thesis, University of Calgary
- Morris DW (1984) Patterns and scale of habitat use in two temperate-zone small mammal faunas. *Can J Zool* 62:(in press)
- Morse DH (1968) A quantitative study of foraging of male and female spruce-woods warblers. *Ecology* 49:779-784
- Morse DH (1980) Behavioral mechanisms in ecology. Harvard University Press, Cambridge
- Robins JD (1971) Differential niche utilization in a grassland sparrow. *Ecology* 52:1065-1070
- Rosenzweig ML (1974) On the evolution of habitat selection. *Proceedings of the First International Congress of Ecology* 401-404
- Rosenzweig ML (1981) A theory of habitat selection. *Ecology* 62:327-335
- Schoener TW (1965) The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19:189-213
- Schoener TW (1967) The ecological significance of sexual dimorphism in the lizard *Anolis conspersus*. *Science* 155:474-477
- Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704-726
- Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185:27-39
- Schoener TW (1977) Competition and the niche. In: *Biology of the reptilia*. Gans C, Tinkle DW (eds) Academic Press, New York pp 35-136
- Selander RK (1966) Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edition. Freeman, San Francisco
- Storer RW (1966) Sexual dimorphism and food habits in three North American accipiters. *Auk* 83:423-436
- Trivers RL (1972) Parental investment and sexual selection. In: *Sexual selection and the descent of man*. Campbell B (ed), Aldine-Atherton, Chicago pp 136-179

Received February 2, 1984