

SMALL MAMMAL USE OF MICROHABITAT REVIEWED

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Small mammal microhabitat research has greatly influenced vertebrate community ecologists. There exists a “microhabitat paradigm” that states that sympatry among small mammal species is enabled by differential use of microhabitat (i.e., microhabitat partitioning). However, several studies have failed to detect microhabitat partitioning, and research has consistently indicated that microhabitat phenomena do not explain larger spatial scale (i.e., macrohabitat) variation. Possible reasons for these difficult to reconcile observations are explored by reviewing and tabulating data from 70 studies. The meaning of the term microhabitat has changed subtly since 1969. This review demonstrates that the existing knowledge of small mammal microhabitat partitioning is highly concentrated among small-scale studies, conducted with modest intensity, that measure microhabitat at inappropriate spatial scales. This concentration of knowledge appears to be an insufficient foundation on which to accept microhabitat partitioning as a widely generalizable phenomenon. The observation that microhabitat phenomena do not explain larger spatial scale variation suggests the importance of underappreciated adaptive mechanisms that relate to the ability of species to coexist, use habitat, and ultimately persist.

Key words: macrohabitat, microhabitat, microhabitat partitioning, small mammal, spatial scale

Small mammals are model organisms for a long-term and robust body of research that influences vertebrate community ecologists to such an extent that today there exists a microhabitat paradigm, holding that sympatry among small mammals is substantially enabled by differential use of microhabitat (Price and Kramer 1984; Reichman and Price 1993). Because of the well-known nature of small mammal microhabitat research (Cody and Diamond 1975; Strong et al. 1984), identification of early papers that use the term is a matter of historical significance. Further, while accumulated microhabitat studies clearly indicate that coexisting species partition habitat, the persistent inability of this research to explain larger spatial scale variation (i.e., macrohabitat) points to the importance of underappreciated ecological interactions.

In this study, I compile data on the level of effort and spatial extent of prior research to better understand the context and limitations of small mammal microhabitat studies. This review will show how the term microhabitat is used differently, thereby introducing imprecision and confounding interpretation of (seeming) microhabitat studies that have tended to reinforce the existing paradigm in preference to alternative hypotheses. Further, data compiled for this review support the conclusion that small mammal microhabitat research is highly concen-

trated among a few species, with data typically collected from a small number of research plots and with a modest level of trapping effort. Each of these conditions introduces limitations into the interpretation of microhabitat data that have been uncritically overlooked.

Authors have defined the terms microhabitat and macrohabitat in different ways. Such definitions and their distinctions, while interesting, are not of critical importance for this review. Morris (1987) accurately defined macrohabitat as the spatial area in which individuals perform all their biological functions and microhabitat as being composed of environmental variables that affect individual behavior.

Manipulative, statistically robust studies have investigated multiple aspects of mechanisms underlying microhabitat partitioning since Rosenzweig and Winakur's (1969) seminal effort. However, careful literature review reveals a widespread inconsistency in use of the term microhabitat that (I believe) leads to deeper misunderstandings. I have observed that some misunderstanding is attributable to an implicit belief that conclusions regarding small mammal microhabitat partitioning are supported by large amounts of data.

A relevant illustration of an excessively broad generalization is the supposition that species' abundance is a function of preferred microhabitat availability (Price and Kramer 1984; Reichman and Price 1993). Is widespread acceptance of such broad conclusions related to a decline in microhabitat research? Does reduced interest result from a belief that small mammal microhabitat research is settled science? Are these conclusions at odds with contrary research in both temperate and desert

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systems in North America (Morris 1987; Jorgensen and Demarais 1999; Orrock et al. 2000)?

Rosenzweig and Winakur (1969) are frequently credited with application of the term microhabitat to small mammal research (Dueser and Shugart 1978). Interestingly, Rosenzweig and Winakur (1969) do not use the term. Rosenzweig and Winakur's work is in the scientific tradition of Lotka (1925), Volterra (1928), and Gause (1934) and parallels Robert MacArthur's work with birds (MacArthur 1964; MacArthur and MacArthur 1961). Thus, microhabitat research is interested primarily in mechanisms of coexistence and competition. It appears that Schoener (1974:30) was the 1st to use the term in a context familiar to small mammal ecologists. Brown (1975) used the term to characterize Brown and Lieberman (1973), but the term microhabitat does not appear in Brown and Lieberman (1973). M'Closkey (1976) used the term in 1976, and by 1978 the term microhabitat had become commonplace (Holbrook 1978; Lemen and Rosenzweig 1978; Price 1978; Stamp and Ohmart 1978; Wondollock 1978). However, even at this time, microhabitat was not used by everyone (M'Closkey 1978), and it is unclear whether anyone was aware of its developing etymology. These inconsistencies demonstrate that at that time microhabitat was being used as a vernacular term and without strict definition.

Although many researchers contributed to development of small mammal microhabitat research, Price's notable paper from 1978 serves as the benchmark signifying acceptance of the concept that microhabitat partitioning substantially enables coexistence among small mammal species. For that reason, closer attention to Price (1978) is warranted. Price initially characterizes Rosenzweig and Winakur (1969) as indicating that "rodents subdivide a habitat resource" (Price 1978:910–911), accurately reflecting the multidimensional nature of habitat and a useful expansion of Schoener's (1974) definition. However, in the same paper, Price introduces the term microhabitat and erroneously attributes it to Rosenzweig and Winakur (1969; Price 1978:911). In the next 4 sentences, Price adopts use of the term microhabitat in place of the less elegant "subdivide a habitat resource" (Price 1978:911). Of further import, in these same 4 sentences, Price (1978:911) further defines microhabitat in terms of structural vegetation, consistent with Schoener (1974) but in lieu of Rosenzweig and Winakur's (1969) antecedent but more general definition. In this way, the definition of microhabitat in the context of small mammal research came to be fixed in terms of a single niche dimension (structural vegetation) while simultaneously maintaining (apparently through reference alone) the interpretative authority of a multidimensional Hutchinsonian niche (Hutchinson 1957, 1959).

By the mid-1980s, Rosenzweig and Winakur's (1969) earlier study was routinely characterized as a microhabitat study (Price and Kramer 1984), although the reader can now appreciate that the term had come to mean something much less than the original authors intended. Prior reviews fail to note the indirect but by then universal adoption of the term microhabitat (Brown et al. 1979; Kotler and Brown 1988; Reichman and Price 1993). Further, the term's acceptance and use is accompanied

by recurrent subtle shifts in definition with nearly every paper published. Price appeared to sense a problem with this as early as 1984, warning that

little progress has been made in determining what it is about different habitats or microhabitats that is ultimately responsible for discrimination on the part of the animals involved. Nonetheless, one often finds authors expressing firm opinions about the basis for microhabitat choice—support for one opinion or the other rests almost entirely on circumstantial evidence that each factor may be of general importance to the biology of rodents and therefore conceivably could affect microhabitat choice. (Price 1984:63–64)

The succinct and tractable apparent meaning of microhabitat has served only to further its misapplication and inconsistent use. The many instances of erroneous attribution to Rosenzweig and Winakur (1969) are evidence of this. Uncritical acceptance of Rosenzweig and Winakur (1969) as microhabitat research is strong evidence that few researchers at the time were thinking critically about the importance of definition and spatial precision.

Several studies do not support the prevailing paradigm. Thompson (1982b) found that direct observation produced results that varied from concurrent livetrapping results. Morris (1984a, 1987) tested the extent to which habitat scale governs abundance of *Peromyscus* and *Microtus* and found that microhabitat measurements were less effective predictors of rodent density than was macrohabitat (Morris 1987). For Morris, spatial scale profoundly influenced habitat use and interpretation of habitat analyses (Morris, 1984a, 1984b, 1987). Further, Morris felt strongly that misunderstanding of scale phenomena had impeded deeper understandings of ecological relationships (Morris 1987). Bowers (1986) investigated shifts in microhabitat use associated with removal of individuals from 3 study populations. He found that shifts in microhabitat use occurred sometimes but not always and that the results of such studies cannot be easily generalized across species or their range (Bowers 1986). Jorgensen and Demarais (1999) found that macrohabitat variables better predicted trap use than did microhabitat variables for 9 of 13 Chihuahuan Desert small mammal species. Notably (as will be discussed later), *Dipodomys merriami* displayed a measurable tendency toward predictability with microhabitat variables. Thompson (1987) found that use of microhabitat determined from seed use did not correspond to patterns revealed by livetrapping. Contrary to expectations resulting from microhabitat studies, Jorgensen et al. (1995) found that rodent species trapped in a desert arroyo, including presumed open-microhabitat specialists, were captured more frequently in patch types characterized by thick vegetation. Root et al. (2002) found evidence that trap-site disturbance could affect use of microhabitat. Finally, Orrock et al. (2000) cited probable agreement with Morris's (1984b) results in the Appalachian Mountains of the United States.

While some of these studies postdate important microhabitat reviews by Kotler and Brown (1988) and Reichman and Price (1993), several do not. As already noted but restated for

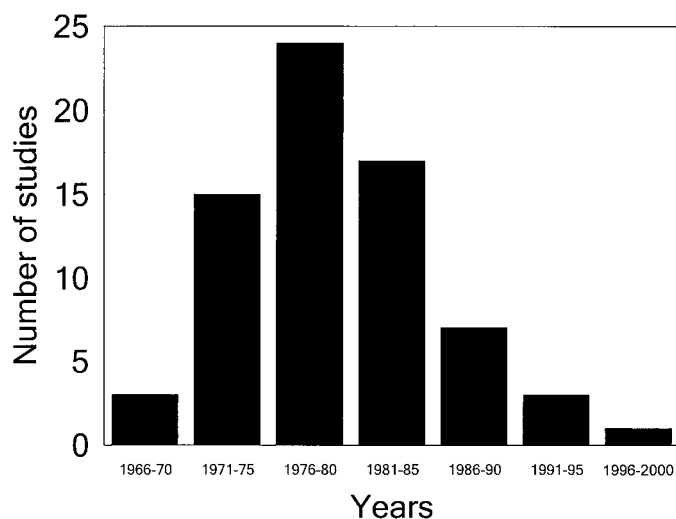


FIG. 1.—Amount of research on small mammal microhabitats has declined from its peak, as shown by number of studies published from 1996 to 2000.

emphasis, of particular concern are broad conclusions that rodent abundance is related to availability of microhabitat (Price and Kramer 1984; Reichman and Price 1993). These conclusions appear to overlook the cautionary themes of Thompson, Morris, and Bowers, leading to an appearance that these studies had little discernable impact on the microhabitat paradigm.

In part, this reaction may result from an implicit belief that foundational studies supporting research on small mammal microhabitat partitioning are extensive and robust. The question then arises: precisely how robust are the studies that are relied on to support the microhabitat paradigm?

METHODS

I examined microhabitat literature on North American small mammals from leading journals. Whereas it is probable that I inadvertently overlooked some papers, the collection of papers is sufficient for me to describe, substantiate, and interpret the patterns investigated. I compiled data from 70 studies published between 1969 and 2000, compiling data on the effort expended and spatial area covered (number of vegetation types investigated, number of grids sampled, trap nights of effort, smallest area of vegetation measured).

In some instances I needed to apply my own judgment to determine which values to enter. For example, in some cases, different types of vegetation were measured with different techniques, each of which used a different spatial scale. In these cases, the smallest spatial scale was used. Also, sometimes investigators used 2 traps at a single trap station, effectively doubling the number of trap nights. In these cases, all traps were counted, effectively doubling the number of trap nights recorded for several studies. Where judgment was needed, an effort was made to err on the side of interpreting the research in the most robust fashion (i.e., smallest spatial scale, most trap nights). In this way, I hoped to ensure that the data set would be conservative and interpretations would be well warranted.

Finally, readers should note that *Perognathus* is used extensively in the microhabitat literature for taxa that now are classified in 2 different genera (*Perognathus* and *Chaetodipus*). In my review, the current taxonomy is applied.

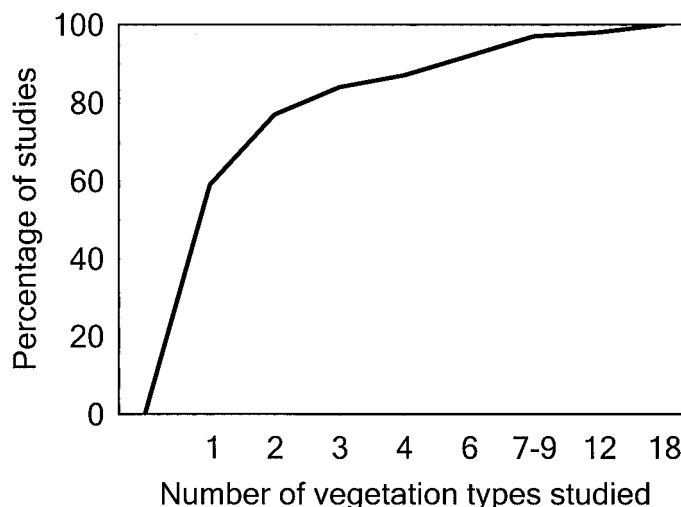


FIG. 2.—Number of vegetation types in which microhabitat studies have been conducted, showing that microhabitat studies are frequently susceptible to confounding by experimentally uncontrolled macrohabitat effects. Of 70 published studies, 59% were conducted in single vegetation types, and 77% were conducted in ≤ 2 types.

RESULTS

Number of published studies peaked during 1976–1980 and has been consistently declining ever since (Fig. 1). Ten studies (14%) fail to identify the number of trapping grids used, 10 (14%) contain descriptions of the vegetation sampling unit for which spatial scale of the vegetation measured and analyzed could not be determined, 19 (27%) use categorical vegetation classes (i.e., under bushes, in the open), and in 26 studies (36%) it is not possible to calculate the precise number of trap nights (Appendix I).

Of the 61 studies that provided information about vegetation type and habitat, 59% were conducted in a single vegetation type, and 77% percent were conducted in no more than 2 vegetation types (Fig. 2). Number of grids used in a study ranged from 1 to 49, and more than 50% of published studies used 3 or fewer trapping grids (Fig. 3). Number of trap nights ranged from 216 to about 455,700, and 50% of studies used $\leq 5,000$ trap nights (Fig. 4). The smallest area of vegetation sampled ranged from 0.1 to 315,000 m²; 49% of studies measured vegetation to no finer a spatial scale than 45 m², leaving only 24% of studies that measured vegetation to a spatial scale of 11 m² or less (Fig. 5). Among all studies, 61 small mammal species were studied. *Dipodomys merriami* was a subject in 36 studies. Fifty percent of published research pertains to 8 small mammal species (*Dipodomys merriami*, *Peromyscus maniculatus*, *P. leucopus*, *Chaetodipus penicillatus*, *Dipodomys ordii*, *Perognathus amplus*, *Chaetodipus baileyi*, and *Reithrodontomys megalotis*; Fig. 6).

DISCUSSION

This review highlights several patterns. In general, microhabitat studies are localized to small spatial scales (Figs. 2 and 3). Most studies are conducted with a modest level of effort

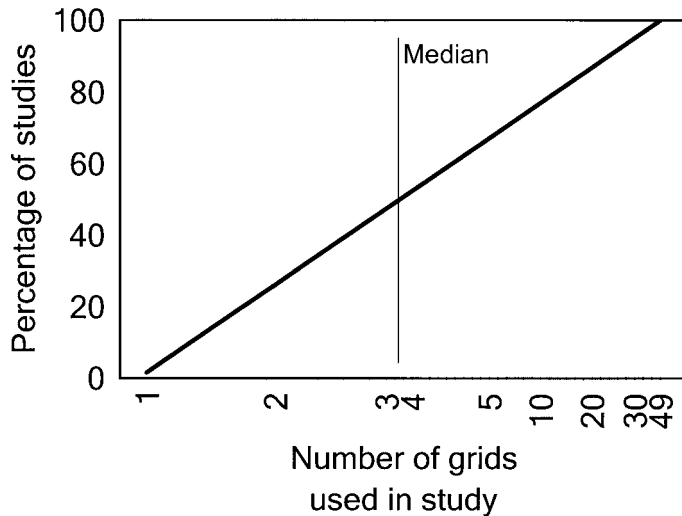


FIG. 3.—Distribution of studies examined by number of trapping grids used, showing that >50% of published studies used ≤ 3 trapping grids and >80% of studies used ≤ 10 trapping grids.

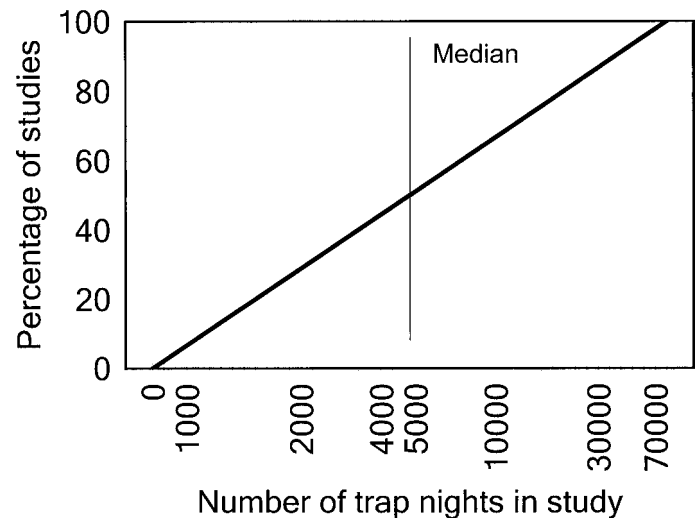


FIG. 4.—Distribution of studies examined by number of trap nights used, showing that >50% of studies used $\leq 5,000$ trap nights of effort. Moreover, >30% of studies used <2,000 trap nights of effort.

(Fig. 4). Frequently, vegetation is not measured (Fig. 5), and only a small subset of small mammal taxa are investigated (Fig. 6). With these limitations in mind, there is a problem reconciling the conclusion that species' density is determined by availability of microhabitat (Reichman and Price 1993) with contrary observations (Jorgensen and Demarais 1999; Morris 1987; Orrock et al. 2000). This review demonstrates that there should be concern regarding the strength of the foundation on which the existing microhabitat paradigm exists.

In part, 1 reason these observations are difficult to reconcile is that too many microhabitat papers report research from single vegetation types using very few trapping grids and modest trapping effort (Figs. 2–4). It is impossible to make general conclusions from these studies. Most particularly, no conclusions regarding spatial scale (i.e., microhabitat) can be supported because small mammal response to similar microhabitats in adjoining vegetation types was not measured and/or replication is open to question. From the data presented in this review, it is too clear that Morris's warning that most studies claiming to document microhabitat partitioning have "mixed macrohabitat and microhabitat effects" (Morris 1984b:1540) is highly pertinent. It should now be clear that a large measure of caution must be exercised when results from most small mammal microhabitat studies are generalized, whether they are for the purposes of conducting lively academic debates, illustrating principles in community ecology, or serving as assumptions for models.

Generalization to applied contexts is of particular concern. Bowers's (1986) observation that the tendency of microhabitat results to vary according to study location has application for efforts to develop and improve mathematical habitat models (Scott et al. 2002). These models promise to provide a significant improvement over traditional range map and county record data (Kiester et al. 1996; Scott et al. 1993). In particular, distribution maps and county record data lack sufficient detail. But how much detail is needed? Theoretically,

assurances that abundance is related to microhabitat availability should be seen as a powerful insight aiding model development. However, when this conclusion is not supported by data, the degree to which locale and microhabitat phenomena interact to affect habitat models remains to be determined.

Conversely, because microhabitat studies have focused closely on individual sites and vegetation types, it is certain that the reported patterns are occurring. However, the more interesting question is why species that select particular microhabitat types in 1 vegetation type do not select identical or similar microhabitat types in adjacent vegetation types. It appears that Bowers's (1986) concern that premature generalization can slow the process by which ecologists investigate interactions in community ecology is valid (Fig. 1). While it is reasonable to expect that the explanation is biological and progress is being made (Bowman et al. 2000a, 2000b, 2001; Jorgensen and Demarais 1999; Knight and Morris 1996; Morris 1992, 1996; Orrock et al. 2000), much remains to be done.

The variability in the literature regarding what constitutes an appropriate spatial scale for microhabitat is worth further discussion. Microhabitats are those components of habitat occurring within an individual animal's home range (Morris 1987). Frequently, this is presented as a bush versus open dichotomy such that many researchers have used categorical variables (i.e., trap under a bush or trap in an open spot; Fig. 4). How much of this variability stems from interpretations of early studies?

The study by Rosenzweig and Winakur (1969) is routinely cited as being microhabitat research (even by me). However, the smallest area of vegetation described by Rosenzweig and Winakur (1969) actually encompasses about 589 m². Is 589 m² an appropriate spatial scale for measuring use of the term microhabitat? While it is certain that the study by Rosenzweig and Winakur (1969) has something to do with microhabitat, it is also reasonable to point out that it is very different from most

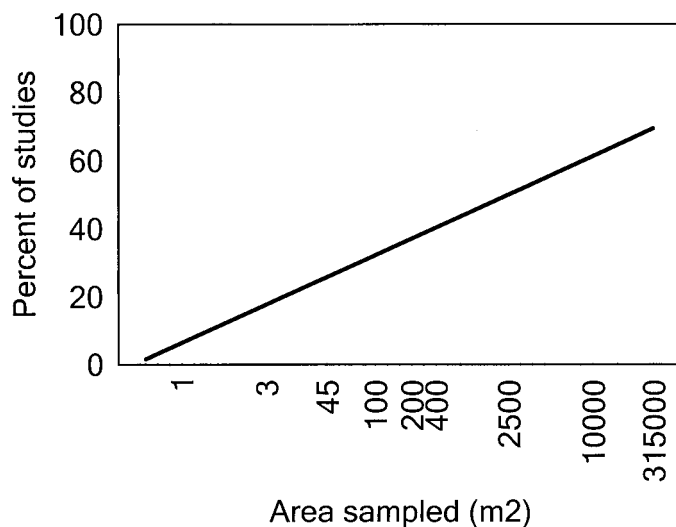


FIG. 5.—Distribution of area studied in microhabitat studies examined, showing that only 22% of studies measured vegetation to a spatial scale of 8 m² or finer, whereas the remaining 78% of studies either assumed categorical variables (33%) and did not measure vegetation at all or measured vegetation to no finer a spatial scale than 45 m² (45%). No studies measured vegetation between 8 and 45 m². (Note: total <100 because of studies using assumed categorical variables.)

other microhabitat studies. I now interpret their study as not actually a microhabitat study. It deals more with patches (Jorgensen et al. 1995). Is the belief that Rosenzweig and Winakur (1969) is a microhabitat study a firm opinion (sensu Price 1984)? The literature leaves this impression (which I believe has strongly influenced interpretation of subsequent research). The concerns clearly expressed by Price in 1984 remain current. Whereas the expression of firm opinion is welcomed, care should be taken to ensure that firm opinion is not substituted for data. Certainly, an objective view leads to the a priori expectation that habitat-use phenomena occurring over 580 m² are probably both quantitatively and qualitatively different than phenomena that occur at <10 m².

Dipodomys merriami is a subject in over 50% of microhabitat studies. When one combines this high level of representation with the additional points that in many localities *D. merriami* is highly abundant and is a species that does partition microhabitat (Jorgensen and Demarais 1999), it is little wonder that many studies claim to document generalized microhabitat partitioning. When the most widespread and abundant representative of the community appears to exhibit microhabitat partitioning, it is not unreasonable to see that interpretation of the resulting research may overly reflect phenomena associated with that species and overly discount factors affecting other species.

To summarize, existing knowledge is highly concentrated among localized (Fig. 2) small-scale studies (Fig. 3), conducted with a modest level of effort (Fig. 4), using assumed microhabitat structure or measuring microhabitat at predominantly inappropriate spatial scales (Fig. 5), with a small subset

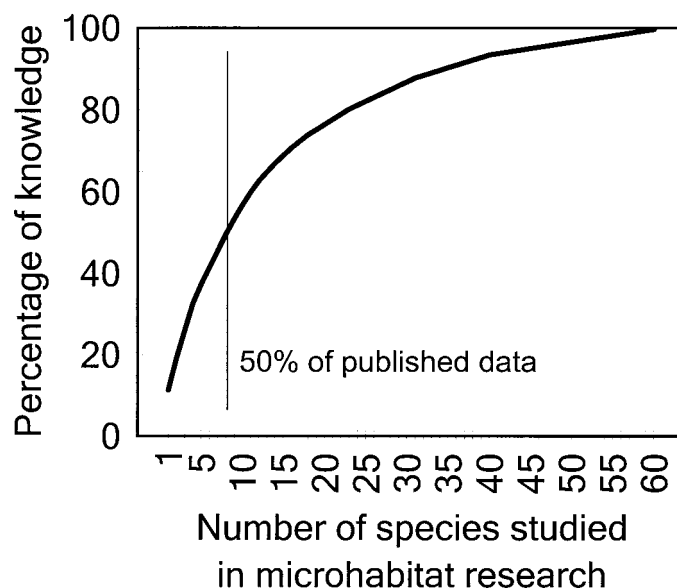


FIG. 6.—Cumulative distribution of studies by number of species studied in microhabitat studies examined. Knowledge is highly concentrated among a few small mammal taxa, with 8 species comprising 50% of published data. The most studied species (*Dipodomys merriami*) accounts for the first 11% of published knowledge, whereas 29 species (almost 50% of those studied) are required to account for the final 11% of published knowledge.

of small mammal taxa (Fig. 6). This concentration of knowledge may be an insufficient foundation on which to accept microhabitat partitioning as a widely occurring phenomenon.

Finally, it is not my intention to cast doubt on or repudiate the substantial body of research that detects microhabitat phenomena. I do seek to strongly caution against generalization of these observations by demonstrating that the microhabitat-partitioning literature for small mammals is taken from research conducted under limited circumstances. Further, more attention needs be drawn to the general (but not universal) observation that microhabitat phenomena do not easily explain larger spatial scale variation. An important reason for drawing attention to this issue is to provoke interest on the part of community ecologists and modelers and encourage them to conduct research that will seek to understand the biological mechanisms that may underlie these observations. Most especially, why do species that select for particular microhabitat types in 1 vegetation type not select for identical or similar microhabitat types in adjacent vegetation types? These observations point to the existence of as yet unappreciated adaptive mechanisms that relate to the ability of species to coexist, use habitat, and ultimately survive.

Recommendations.—Perhaps the most important item highlighted in this review is the need for a much greater degree of awareness concerning the scope, uncertainty, and potential application of the existing microhabitat research. At this time, this research does little to inform applied science and management needs that typically are more concerned with populations than individuals, and this review makes it clear that

the relevance of the existing microhabitat research to population questions is very uncertain.

At the least, efforts to expand the potential application of microhabitat data via modeling or management would involve research conducted in 2 vegetation types, preferably more. While I do not think it is advisable to offer specific guidance for number of trapping grids and trapping effort, microhabitat research has not been sensitive to issues of replication and thus has mistaken phenomena associated with individuals for phenomena that can be generalized to populations and species. Appropriate replication is a more important question than number of grids or number of trap nights, although among mammalogists these are frequently used as surrogates to establish initially acceptable evidence of credible effort. It should be self-evident that microhabitat research needs to measure habitat structure at a fine spatial scale. For example, whereas live traps are frequently used to sample, the scale of the measurement should be chosen to be relevant to the scale of the sampling. Practitioners need to put careful thought into this before they begin their research.

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APPENDIX I

Studies analyzed for this review. Where available, data include number of vegetation types, number of trapping grids, number of trap nights of effort, area of vegetation sampled (Area), and number of species studied (na = data not available).

Reference	Vegetation types	Number of grids	Number of trap nights ^a	Area (m ²)	Species
Abramsky et al. (1979)	1	8	10,000	15,120	5
Beatley (1976)	6	8	8	About 33,000	2
Bowers (1982)	1	na	na	na	3
Bowers (1986)	3	3	1	12,600	3
Bowers (1988)	1	20	Cat ^b	1,000	2
Brown (1973)	18		Cat ^b		18
Brown (1989)	1	4	Cat ^b	About 1,568	13
Brown and Lieberman (1973)	1		Cat ^b		18
Brown and Munger (1985)	1	24	2,500	68,159	11
Brown et al. (1972)	1	10	2,500	na	1
Douglas (1976)	1	4	<1	na	2
Dueser and Shugart (1978)	3	12	1–314	9,696	4
Grant (1971)	1	3	4,000	na	2
Hallett (1982)	1	1	38		12
Hansen and Batzli (1978)	1	2		18,720	1
Hansen and Batzli (1979)	1	4	3,600	18,432	1
Harris (1984)	2	2	Cat ^b	1,360	4
Harris (1986)	1	2	Cat ^b	About 8,000	2
Hay and Fuller (1981)	na	1	Cat ^b	216	2
Heske et al. (1994)	1	24	2,500	About 455,700	10
Holbrook (1978)	3	30	1	4,200	4
Holbrook (1979)	4	6	15,000	18,600	3
Hutto (1978)	na	1	na	na	2
Jorgensen and Demarais (1999)	6	48	3	69,120	13
Jorgensen et al. (1995)	1	1	Cat ^b	5,000	8
Kaufman and Felharty (1974)	12	12	<1	2,880	9
Kaufman et al. (1983)	8	1	177	843	1
Kaufman et al. (1983)	?	1	Cat ^b	1,498	1
Kenagy (1973)	1	4	na		3
Kotler (1984)	1	2	10,000	7,000	6
Lemen (1978)	1				3
Lemen and Rosenzweig (1978)	1		Cat ^b		2
Longland and Price (1991)	1	1	na	na	5
M'Closkey (1975a)	9		900–11,025		3
M'Closkey (1975b)	2	2	4	na	1
M'Closkey (1976a)	1	1	45		9

APPENDIX I.—Continued.

Reference	Vegetation types	Number of grids	Number of trap nights ^a	Area (m ²)	Species
M'Closkey (1976b)	1		100	na	1
M'Closkey (1978)	>1	21	78	About 2,646	4
M'Closkey and Fieldwick (1975)	1	1	3	1,000	2
M'Closkey and Lajoie (1975)	7	12	2,600		2
Meserve (1976)	1	1	57	About 7,926	6
Morris (1979)	2	4	1–177	About 5,000	6
Morris (1984a)	2	2	1–177	1,620	2
Morris (1984b)	6		0.2–282		About 4
Morris (1987)	3	4	1–177		2
Myton (1974)	1	1	400	18,228	3
Price (1978)	1	1	200	2,376	4
Price (1978)	1	6	200	About 4,992	4
Price (1978)	1	49	113	2,044	4
Price and Kramer (1984)	1	2	Cat ^b	1,089	6
Price and Waser (1985)	1	1	Cat ^b	na	4
Price et al. (1984)	1	2	Cat ^b	2,800	5
Rebar and Conley (1983)	1	3	78	2,160	2
Reichman (1975)	2	2	315,000	About 30,000	4
Reichman and Oberstein (1977)	na	1	na	na	2
Ribble and Samson (1987)	4	5	1–400	8,400	7
Rosenzweig (1973)	2	34	801	1,296	2
Rosenzweig and Sterner (1970)	na	na	na	na	7
Rosenzweig and Winakur (1969)	1	26	589	3,975	10
Schroder and Rosenzweig (1975)	2	10	200,000		2
Shure (1970)	1	4	Cat ^b	6,979	5
Smigel and Rosenzweig (1974)	1	1	Cat ^b	na	2
Stamp and Ohmart (1978)	2		491	56,520	4
Thompson (1982a)	2	2	Cat ^b	1,728	3
Thompson (1982b)	1	4	Cat ^b	na	2
Thompson (1987)	1	4	2,500	2,304	1
Vickery (1981)	>1	10	491	na	3
Whitford (1976)	2	5		552,000	15
Whitford et al. (1978)	1	2	90,000	1,200	10
Wondolleck (1978)	1	2	Cat ^b	12,936	4

^a Calculated as number of traps per station × number of nights of trapping.

^b Cat = categorical classes when vegetation not measured (e.g., under bush, in open).