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Ed.

Evidence for competition in small rodents

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Summary. Many studies of interspecific competition in small rodent communities suffer from methodological shortcomings. They may have been done in small enclosures less than one home range in size or have lacked replication and proper controls. We cannot yet determine how important interspecific competition is in small rodent community organization.

Reviews play a major role in the development of a field. Throughout the last ten years a variety of general reviews about interspecific competition has appeared in the literature (Connell 1975, 1983, Diamond 1978, Birch 1979, Lawton and Strong 1981, Schoener 1982, 1983, Simberloff 1982). One outstanding feature of these reviews is the difference between the sets of evidence included to emphasize the relevance or irrelevance of competition in nature. To a certain extent the selection of evidence depends on which side of the controversy the reviewers have been working. More important, though, is that the evidence presented is selected according to their different scientific standards' one ecologist's evidence is another's fairy tale.

The general trend of these reviews is to include research done with more rigorous experimental designs that include replicates and contemporaneous controls, and to discard simple post hoc explanations. Unfortunately, the trend is not consistent: some reviews dismiss or omit important articles that contradict the evidence or give alternative explanations, others include articles that have been severely criticized before. An example of the first error is the weakness of natural niche shifts and character displacement as evidence for competition. This has been criticized (Grant 1972a, 1978, Connell 1975) because of the lack of controls and therefore the variety of alternative explanations that account for the same patterns, but these examples continue being used as evidence in favor of competitive interactions (Diamond 1978, 1983). An example of the second error is the Koplin and Hoffmann (1968) study of *Microtus montanus* and *M. pennsylvanicus*. This study has been criticized in earlier reviews (Grant 1972b, Connell 1975, Birch 1979) as an inadequate test of the competition hypothesis, because of differences in densities and conditions of the plots. The experimental plot in this study was fenced and not grazed by bison and had 4 to 5 times more animals than the control. In spite of such criticism this study is continually used as evidence for competition among voles (Schoener 1982, 1983).

Connell (1983) pointed out that because of the status of experimental evidence in ecology, people tend to accept the conclusions of experimental studies uncritically. We agree with him and feel that the conclusion drawn from the 18 studies selected in Schoener's review (1983) misrepresents the state of the art in small mammal research. This author seems oblivious of the many methodological shortcomings in his selection of studies on competition among rodents (mice). One-third (6 of 18) of the studies used by Schoener (1983) were done in small enclosures or exclosures (Grant 1969, 1971, Morris and Grant 1972, Hoffmeyer 1973, Price 1978, Munger and Brown 1981). In all but one study (Munger and Brown 1981) the resident population was trapped out and individuals caught somewhere else and kept in captivity for different periods of time were introduced into the enclosure. Once there, the animals were exposed to a novel environment and unknown individuals. Their movements were highly restricted. In most cases the home ranges of the individuals introduced were larger than the enclosures. For example, the home range of deer mice (*Peromyscus maniculatus*) ranges for 0.28 to 1.89 hectares (Blair 1940, Eisenberg 1981, Taitt 1981). Yet Grant (1971) used enclosures of only 0.4 ha. The

Tab. 1. Rodent (mice) studies selected by Schoener (1983). Only 4 (*) out of 18 were done in natural conditions with rigourous experimental designs. For studies not done under natural conditions the area (ha) of the enclosure is given in parentheses.

Authors	Species	Natural	Contemporary control	Replicates
Joule and Jameson 1972	*Sigmodon hispidus* *Reithrodontomys fulvescens* *Oryzomys palustris*	yes	yes	no
Morris and Grant 1972	*Microtus pennsylvanicus* *Clethrionomys gapperi*	no (0.8)	no	no
Grant 1969	*M. pennsylvanicus* *C. gapperi*	no (0.4)	yes	no
Grant 1971	*M. pennsylvanicus* *P. maniculatus*	no (0.4)	yes	no
DeLong 1966	*Mus musculus* *Microtus californicus*	yes	yes	no
Koplin and Hoffmann 1968	*M. pennsylvanicus* *M. montanus*	yes	yes	no
Holbrook 1979	*Peromyscus boylii* *P. maniculatus* *Neotoma stephensi*	yes	yes	yes *
Hoffmeyer 1973	*Apodemus flavicollis* *A. sylvaticus*	no (0.015)	no	no
Price 1978	*Dipodomys merriami* *Perognathus baileyi* *P. penicillatus* *P. amplus*	no (0.26–0.34)	yes	yes
Schroder and Rosenzweig 1975	*Dipodomys merriami* *D. ordii*	yes	yes	yes *
Abramsky et al. 1979	*Microtus orchrogaster* *Reithrodontomys megalotis* *P. maniculatus*	yes	yes	no
Sheppe 1967	*P. maniculatus* *M. musculus*	no (food shed)	no	no
Redfield et al. 1977	*P. maniculatus* *Microtus townsendii* *M. oregoni*	yes	yes	yes *
Montgomery 1981	*A. sylvaticus* *A. flavicollis*	yes	yes	no
Munger and Brown 1981	*Dipodomys spectabilis* *D. merriami* *Dipodomys ordi* *Perognathus penicillatus* *P. flavus* *R. megalotis* *P. maniculatus* *Peromyscus eremicus* *Onychomys leucogaster* *O. torridus*	no (0.25)	yes	yes
Cameron 1977 Kincaid and Cameron 1982 Cameron and Kincaid 1982	*Sigmodon hsipidus* *Reithrodontomys fulvescens*	yes	yes	yes *
Abramsky and Sellah 1982	*Gerbillus allenby* *Meriones tristrami*	yes	yes	no
Gliwicz 1981	*Apodemus flavicollis* *Apodemus agrarius* *Clethrionomys glareolus*	yes	yes	no

enclosures were furthermore divided into two habitats where deer mice habitat represented 0.2 ha. Kangaroo rats (*Dipodomys merriami*) have an average home range size of 1.92 ha (Eisenberg 1981). Yet Price (1978) used enclosures of only 0.34 ha. Movements of 5 and 9.5 km have been recorded in a closely related species of kangaroo rat (Schroder and Rosenzweig 1975). If the animals have non-overlapping home ranges the problem is even worse. The homing behavior of some of these rodents is well developed and movements from 100 to 300 m are not uncommon (Stickel 1968).

When the major parameters estimated in these experiments depend on the behavior of the animals it seems that these enclosure restrictions could affect the

results significantly. Krebs et al. (1969) have shown that even enclosures of 0.8 ha affect the dynamics of vole populations. Furthermore, enclosures restrict other species such as predators that may play an important role in the system (Connell 1975).

Another important drawback not endemic to small mammal research but evident in a major part of ecological research is the lack of rigorous experimental designs (Hayne 1978, Hurlbert 1984). More than half (10) of the rodent studies chosen were done with no replicates and three had no contemporary controls (Tab. 1).

Schoener (1983) interprets these studies as detecting interspecific competition if there was an effect on any of several parameters estimated, even when the overall conclusion of the study was that competition was unimportant (Cameron 1977, Kincaid and Cameron 1982). He fails to mention how many parameters did not change. If we bear in mind that at least in small mammal studies most of the effects selected by Schoener have not been replicated, some had no controls and many were obtained in highly artificial enclosure conditions, his general conclusion that 90% of the studies demonstrate som competition may be very misleading.

If the purpose of a review is to show the pervasive importance of competition in ecological systems, as Schoener (1983) states in his summary, we find that at least in the field of small mammal research that conclusion is unsupported. Competition has been documented in some small mammal communities (Redfield et al. 1977, Holbrook 1979), but not in others (Schroder and Rosenzweig 1975, Kincaid and Cameron 1982). Until more careful field experiments are carried out we can decide neither how frequently competition occurs in nature nor how important it is in relation to other processes. Our intention is not to discourage experimental work but to encourage better experimental disigns.

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When should a field experiment be counted?: a reply to Galindo and Krebs

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In my review of field experiments on interspecific competition (Schoener 1983), 18 of 164 studies were of small rodents. Galindo and Krebs (1986) claim that only 4 of these 18 studies "were done in natural conditions with rigorous experimental designs", and that therefore my conclusion "that 90% of the studies demonstrate some competition may be very misleading." I offer a reply, first, to two specific claims which are at best themselves misleading, and second, to the general set of criteria that Galindo and Krebs argue as necessary for an experiment to be counted in a review.

Specific claims. 1) Galindo and Krebs write that Schoener (1983) "fails to mention how many parameters did not change" as a result of experimental perturbation. This is false. In Tab. 1 (Schoener 1983), all parameters (under "effects") that did not change are enclosed in brackets. For example in the studies by Cameron and colleagues mentioned by Galindo and Krebs, I noted that habitat use but not density or food use was affected, and that only 1 of 2 species was affected. It is correct that I did not weight studies by how many effects were found, but this is a different issue (see Schoener 1985) and not the claim of Galindo and Krebs.

2) Galindo and Krebs write "Connell (1983) pointed out that because of the status of experimental evidence in ecology, people tend to accept the conclusions of experimental studies uncritically. We agree with him and feel that the conclusion drawn from the 18 studies selected in Schoener's review (1983) misrepresents the state of the art in small mammal research." The implication is that Connell (1983) has not misrepresented the "state of the art." Connell included those studies he considered valid that were published in 6 journals over the period 1974–1982. In fact, all of the 7 studies from Connell's journals and years used in my review are also included in Connells' review (except part of Price [1978], but for noncontemporaneous controls, not for the shortcoming claimed by Galindo and Krebs). A second implication is that I have "selected" studies. In fact, as stated several times (Schoener 1983, 1985), I tried to be exhaustive. Apparently I was relatively successful, as up to now only 4 studies meeting my criteria have been pointed out to me as absent from my review.

General criteria. Galindo and Krebs list three criticisms of rodent field-competition experiments in particular, and by implication, of field experiments in general; one of these is at least two criticisms, and I would like therefore to arrange my reply in four parts.

1) *Enclosures too small.* In 6 of 18 studies, Galindo and Krebs argue that the enclosures used are too small; in all but one of these, they are smaller than the average individual home-range area of the manipulated species. This criticism would seem more interesting for studies testing for a density effect than those testing for effects on habitat preference. In the latter case, one almost has a behavioral experiment in the field, and virtually all behavioral experiments on terrestrial vertebrates would be invalid were their spatial requirement adhered to themselves. Indeed, most of the 6 experiments faulted focus on habitat preferences. While it is more plausible that conclusions about population density are called into question when enclosures are very small, Galindo and Krebs give no argument for this, and one must ask how