PEROMYSCUS NEWSLETTER

NUMBER TWENTY

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Cover: The "Mother of all *Peromyscus* Newsletter covers"

ISSUE #20

Well, we hit another milestone with *PEROMYSCUS NEWSLETTER* **#20**. Our cover displays the initial ten years of covers. While we have strived to retain an informal tone to *PN*, we have gradually made improvements, at the same time keeping costs of production in check. Our first few issues were done with a dot matrix printer and produced with the office copier. Janet and I individually assembled and stapled each copy. Of course, we had fewer subscribers then. We ran 175 copies of Number 1. Currently, we run 750 copies and have about 675 names on the mailing list. Beginning with Issue #19, thanks to commercial printing, we have improved the paper quality and are able to produce full-color photography on our covers at little increase in expense. Production and mailing costs have averaged about $ 1,000 per issue in the past few years. The University of South Carolina Biological Sciences Department graciously subsidizes half of this cost and the remainder is charged to the Stock Center Revenue Account. Thus, we have been fortunate to be able to provide *PN* free to our readers.

In this issue we conclude our two-installment account of "*Peromyscus* and Electrophoresis". The initial installment, in *PN* #18, recalled the early days of protein electrophoresis (1960-1970) and the efforts of David Rasmussen, Charles Foreman and others. In the second part, we review the "heyday" (1971-1986) and the contributions of the many *Peromyscus* population geneticists and systematists who were active during that stimulating period. We thank Earl Zimmerman, Mike Smith, Bill Kilpatrick and John Avise for providing interesting background information and for corrections and additions to the manuscript. We also thank the various individuals who provided photographs of themselves.

Once again we urge our readers to send us informal accounts and interim results of research being conducted with *Peromyscus*, whether in the lab or field. Even though, as an NSF-funded genetic stock center, we tend to place some emphasis on genetics, *PN* is for all "peromyscologists". We want to keep it that way. About 75% of utilization of animals from the *Peromyscus* Stock Center is for non-genetic (*i.e.* ecological, environmental, biomedical and behavioral) research.

Deadline for Issue #21 is 15 March 1996!

And don't forget our e-mail address: **peromyscus@stkctr.biol.sc.edu**

Enjoy!

WD

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NEWS, COMMENT and ANNOUNCEMENTS

Sergey Morzunov of Centers for Disease Control (CDC) in Atlanta has been sequencing hantaviral genomes to construct phylograms which can be compared with those of host species (*Peromyscus maniculatus* and *P. leucopus*) derived from mtDNA D-loop fragment sequences. Initial evidence indicating correspondence of phylogenies is supportive of co-evolution of the virus and primary host. See his contribution on p. 25.

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At the annual meeting of the American Society of Mammalogists held at the University of Vermont in Burlington "*leucopus* lager" flowed in abundance courtesy of the host institution. Papers and posters on *Peromyscus* were likewise abundant, with about 20 presented. **Kathryn Gubista**'s paper, "Litter size of *Peromyscus leucopus*: Effects of food limitation" won the ASM award for graduate student research. **Bill Kilpatrick** was chairman of the local committee for the meeting.

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Ability to distinguish <u>Peromyscus californicus</u> from house mouse helped the redoubtable TV dectective, **Columbo**, solve a murder mystery in the May 8th episode.

Bruce Buttler sends his e-mail address (**buttler@hp9000.eita8net.com**) for those who would like him to search his extensive *Peromyscus* database in order to generate individualized bibliographies (free of charge). Bruce has compiled comprehensive bibliographies on *Peromyscus* genetics, reproduction, dispersal, use in environmental monitoring, and predation studies.

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We were saddened to learn of the recent deaths of two individuals who interacted with many of us involved with Peromyscus *research.* **David Klingener** *of the University of Massachusetts passed away this summer. David wrote the "Anatomy" chapter in King,s* **Biology of Peromyscus** *and once served as feature article editor for* **Journal of Mammalogy.**

Vern Chapman *of Roswell Park Memorial Institute died suddenly of a cerebral hemorrhage while attending a professional meeting in Japan. Vern was a mouse geneticist who was among the first to use wild* Mus *of various species for genetic research. He had a collateral interest in* Peromyscus *genetics, as well.*

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Charles Handley of the Department of Mammals at Smithsonian is writing an account of *Peromyscus maniculatus* for **Don Wilson's** forthcoming *Complete Book of North American Mammals.*

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ANNOUNCEMENT

Records of the mammal collection of the Denver Museum of Natural History have been computerized, thus increasing accessibility for scientific research. This collection includes more than 1000 specimens (study skins, skulls and skeletons of *Peromyscus boylii, P. crinitus, P. eremicus, P. leucopus, P. maniculatus, P. nasutus, and P. truei*, most are from Colorado, but we also have material from Arizona, New Mexico, Texas, and Utah. Researchers interested in examining specimens should contact Dr. Cheri Jones, Denver Museum of Natural History, 2001 Colorado Blvd., Denver CO 802-5798.

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Thomas E. Nupp, Purdue University Forestry College, is currently working on a Ph.D. research project examining the effects of forest fragmentation in Indiana on the community of granivorous rodents. Some of his initial results were reported at the Mammalogists meeting at Burlington in June.

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Mary Klein, of Yale University, graciously sent three skins of the offspring of the *beige* X *blonde* genetic cross for the Stock Center reference collection.

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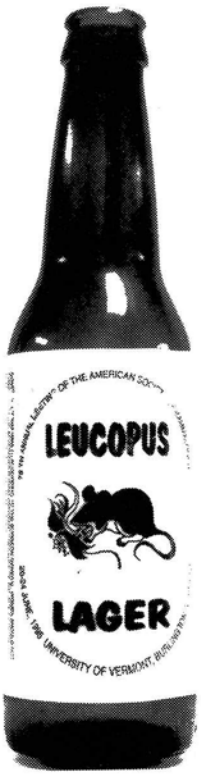

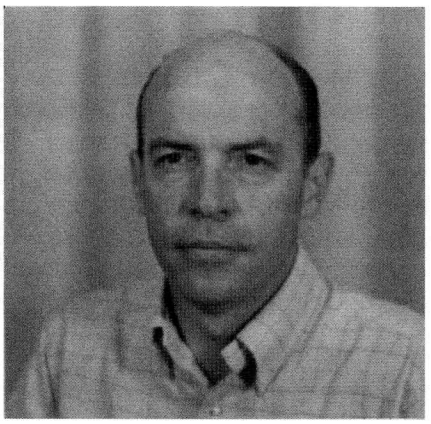

Bob Selander

Mike Smith

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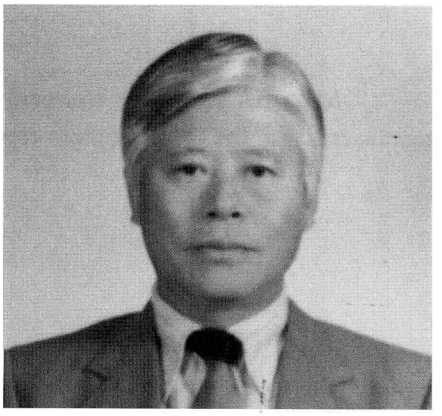

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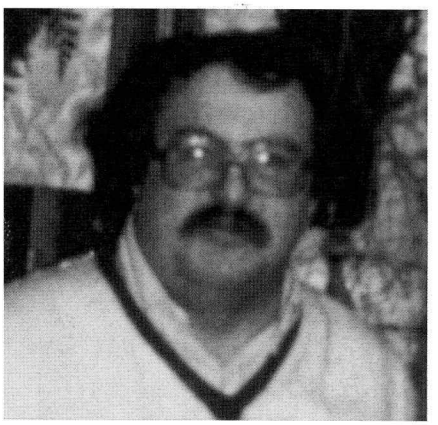

Bill Kilpatrick

PEROMYSCUS AND ELECTROPHORESIS:

THE HEYDAY 1971 - 1986

The discovery that species in nature exhibit much higher levels of protein polymorphism, as detected by starch gel electrophoresis, than had been previously suspected (Lewontin and Hubby, 1966) ignited a torrent of research to explore and interpret this newfound diversity with all manner of organisms. *Peromyscus* was not an exception. During the two decades beginning in 1971, more than 40 published papers recorded natural polymorphism of protein variants (="biochemical polymorphism") in the genus. Here, in the second installment of our two-part account of "*Peromyscus* and Electrophoresis", we review that exciting period in which many of our readers participated.

During the decade prior to 1971 several "pioneers" had examined polymorphisms for individual proteins, particularly serum proteins and hemoglobins (See *PN#*18), but no large scale studies on the order of that of Lewontin and Hubby had been conducted using *Peromyscus*. The first major allozyme survey in *Peromyscus* resulted from a collaboration between Robert Selander, then at the University of Texas, and Michael Smith of the Savannah River Ecology Laboratory (SREL). Mike Smith had worked with *Peromyscus* since 1960 when, as a master's degree student at San Diego State, he studied behavioral discrimination between *P. californicus* and *P. eremicus* (Smith, 1965). After completing his Ph.D. in 1966 at the University of Florida, where he analyzed population structure and ecology of *P. polionotus*, he joined the staff at SREL where several prior field studies of oldfield mice had been conducted. Thus, Mike was well situated to undertake *Peromyscus* ecological genetics research.

At a 1969 meeting at the University of Georgia Mike engaged Selander in a discussion of population genetics of rodents. Bob Selander and his associates had recently completed studies of protein polymorphism and genic heterozygosity in American and European house mouse (*Mus*) populations (Selander and Yang, 1969; Selander *et al.*, 1969). As a result of this discussion, Selander and Smith agreed upon a collaboration to conduct an analogous study of *P. polionotus* represented by several geographic races (nominal subspecies) in the southeastern U.S. Smith and his SREL colleagues would collect the animals from numerous localities and ship them live to Austin where the electrophoretic typing would be conducted, principally by Selander's laboratory coordinator, Suh Y. Yang and Walter Johnson, a postdoctoral associate. Smith subsequently spent a sabbatical leave with Selander to learn electrophoretic techniques first hand. In the course of the *Mus* studies, Yang had perfected the methodology and adapted it for use with small vertebrates. Starch gel electrophoretic conditions, buffers and stain visualization procedures soon were optimized and became available for numerous enzymes and other proteins. These methods could be applied directly to *Peromyscus* and, with modification, to most vertebrates.

The initial fruit of this collaboration was a lengthy report, "Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse, *Peromyscus polionotus*", published in the University of Texas *Studies in Genetics* (Selander *et al.*, 1971). This landmark paper, the first in a series of papers, is cited in nearly every subsequent report on allozymes in

Peromyscus, and Yang's recipes, included as an appendix, became widely used. The paper eventually became a "citation classic" referenced more than 1000 times. Thirty proteins were surveyed for 30 distinct populations. About half of the proteins were polymorphic in one or more of the populations. Esterases and phosphoglucose isomerases tended to be more polymorphic than other proteins. Insular populations had lower mean heterozygosities than those on the mainland. Overall heterozygosity generally increased from ~5.0 to ~8.6% along a north-to-south gradient, when isolated Gulf Coastal populations were excluded. There was no pronounced correspondence between allozyme allele distribution and formal subspecific boundaries. These observations were consistent with those from allozyme studies in other organisms.

Initial reaction to the Selander/Smith paper was mixed. A few who had been working with protein variation in *Peromyscus* felt that the Texas-SREL group had encroached upon their own on-going projects, and this provoked some ire. A more cogent criticism of this and similar subsequent studies was the assumption that each protein electromorph represented an "allele" when there had been no formal genetic analysis to support the contention. If this were the case, and some bands on the gels were epigenetic, the level of heterozygosity could be overestimated. A counterargument was that electrophoresis did not detect "hidden" polymorphism resulting from isoallelic mutations which did not produce a net charge change (Aquadro and Avise, 1982) and, thus, the true heterozygosity was likely to be underestimated. As evidence developed that epigenetic protein modification sometimes produced changes in electrophoretic mobility (*e.g.* Spooner and Baxter, 1969), a more conservative approach treated electromorphs as products of "presumptive alleles".

The Selander/Smith paper was soon followed by several similar reports for other species of *Peromyscus* by these investigators and others who were early to board the bandwagon. Most of these followed the pattern established by Lewontin and Hubby and the Texas-SREL group, *i.e.* a sample of typically 10 or more individuals from each of a dozen or more geographic locations would each be screened for a panel of 10 to 40 proteins, of which, usually half or more demonstrated intra- or interpopulational polymorphism (isozymes). Most of the proteins were alloenzymes distinguished by substrate specificity, stain reactions and electrophoretic mobility. Soluble tissue esterases, phosphoglucomutases, phosphoisomerases, dehydrogenases, peptidases, phophorylases and aspartate aminotransferase, along with hemoglobin and transferrin, were typically among the proteins scored. In 1973 and '74 the next three papers in the Selander/Smith "Biochemical polymorphism and systematics ...." series appeared with surveys of (III) the Florida mouse (*P. floridanus*), (V) subgenus *Haplomylomys* and (VI) the *P. boylii* species group. [Papers II and IV in the series were planned, but never published.] A paper by Robbins *et al.* (1985) on the *P. leucopus* group concluded the collaborative project more than a decade later. The first author on the *Haplomylomys* and *P. boylii* papers was John Avise. John, a native of Michigan and University of Michigan graduate, had obtained a master's degree with Selander at Texas, researching allozyme polymorphism in cave and surface dwelling populations of the fish, *Astyanax mexicanus*. Subsequently, he joined Smith at SREL and continued allozyme studies on sunfishes (*Lepomis*) and joined the collaborative analysis of *Peromyscus* populations. In 1973 John moved on to U.C.-Davis for his Ph.D., and from there, in 1975, into a faculty position at the University of Georgia, initially in Zoology and later, in 1980, in the newly organized Genetics Department. At Georgia, John continued to conduct evolutionary genetic research with *Peromyscus* and numerous other animals.

During the the mid-1970's others also were beginning to survey biochemical polymorphism in *Peromyscus*. At M.D. Anderson Institutue in Houston, James Mascarello and Charles Shaw (1973) surveyed eight *Peromyscus* species for 14 enzyme loci. Of these loci, all but three were polymorphic within the genus. Gerald Johnson and Robert Packard (1974), of the Texas Tech University faculty, screened four populations of the *P. truei* species group for 14 protein loci, of which 12 were polymorphic. This survey provided support for *P. comanche* as specifically distinct from *P. truei* and *P. (nasutus=) difficilis*. Ayesha Gill (1976), then at UCLA, screened for protein electrophoretic variants at 28 loci in *P. maniculatus* populations on four Channel Islands off southern California. Fifteen of the loci were variable. She found that the genetic distances were consistent with the geological history of the islands. Mice from the northern island populations were more similar to the mainland population than were those of the southern group.

By the mid-1970s the neutralist-selectionist controversy, which arose in response to the discovery of near-ubiquitous protein polymorphism in natural populations, was raging within the ranks of evolutionary genetics. Selectionists generally argued that heterozygosity *per se* contributed to fitness due to overdominance or co-adapted gene complexes or both, and was subject to natural selection. These issues were also widely discussed with respect to *Peromyscus* at meetings of the American Society of Mammalogists, the Society for the Study of Evolution and the AIBS, and in various papers (*e.g.* Selander and Kaufman, 1973; Smith *et al.*, 1974). *Peromyscus* researchers tended to be selectionists in the neo-darwinian tradition. Methodological questions - "Which buffer? What voltage? pH?" - abounded. The significance and utility of protein polymorphism for systematics (Avise, 1974) also aroused immense interest, giving rise to the "find 'em and grind 'em" school of *Peromyscus* systematists. Statistical estimates of similarity and genetic distance (*e.g.* Rogers, 1972; Nei, 1971) were extensively applied to "genic" (= protein electrophoretic) traits to construct phylogenies, which generally coincided well with traditional morphologically-based systematics (Stangl and Baker, 1984). Increasingly, cladistic procedures and terminology were applied to *Peromyscus* systematics. The relationship of protein heterozygosity to effective population size and to "environmental grain" were other matters of considerable interest to contemporary mammalian ecological geneticists. A sense of excitement pervaded the field. As John Avise noted, "Those were heady times!"

While the Selander/Smith/Avise group dominated the field of *Peromyscus* population genetics during the early 1970s, a second focus of research was being developed at North Texas State University (now North Texas University) at Denton by Earl Zimmerman and his graduate student, C. William Kilpatrick. Earl had received his degree at the University of Illinois in 1970, having worked with cytogenetics under the direction of M. Raymond Lee. At Illinois, Earl had done his dissertation work on cytogenetics of *Sigmodon*. He assumed a faculty position at NTU directly out of graduate school, and began exploring research options at his new institution. Meanwhile Bill Kilpatrick, who had received his BS and MS degrees at Midwestern University where he was advised by Walter Dalquest, had enrolled as a Ph.D. candidate at North Texas intending to work with a faculty member who shortly resigned, leaving Bill without a research adviser. Bill approached Earl, who was only a year older than himself, about working with him since they shared an interest in vertebrate evolution and population genetics. Bill had experience with the *P. boylii* group from his master's work, and intended to expand that into a traditional morphological, karyological and zoogeographical study. But at the 1971 meeting of the American Society of Mammalogists at Vancouver, papers and discussions on electrophoresis excited his

interest and suggested a means to resolve issues raised by chromosome variation reported in the *boylii* group (Lee *et al.* 1972). Bill mastered protein electrophoresis, with some advice from Neil Jensen and experience in a comparative physiology course.

Earl and Bill soon established a strong partnership that, over the next several years, generated several key papers in *Peromyscus* evolutionary genetics and systematics . Initially, Bill conducted most of the electrophoresis and Earl contributed his chromosomal expertise. They focussed primarily on the *P. boylii* and *P. truei* species groups, since they contained species and subspecies with uncertain affinities, particularly in Mexico. Billy Hart, a graduate student who joined Zimmerman in the spring of 1971, also contributed substantially to this work. The first two papers from the UNT group appeared in 1975 and a third the following year. Like others, Kilpatrick and Zimmerman evaluated the existing systematics against phylogenies they generated from their biochemical similarity data, and they considered the mechanisms contributing to overall heterozygosity differences among populations. During this time Bill and Earl (1976) also found extensive hemoglobin polymorphism in *P. pectoralis*. Zimmerman, Kilpatrick and Hart synthesized their results with existing genic data from others in a frequently cited 1978 paper in *Evolution*, "The genetics of speciation in the rodent genus *Peromyscus*".

Still others entered the *Peromyscus* allozyme game during the mid-to-late 1970s. Robert Browne (1977), of the University of Dayton, compared Lake Erie mainland and insular populations of *P. leucopus*, finding that the island populations were about 1% less heterozygous and 11% less polymorphic than those of the mainland. Eric Loudenslager (1978), then at the University of Wyoming, analysed the genetic structure of nine demes of *P. maniculatus nebrascensis* in Wyoming, finding polymorphism at 13 of 14 presumptive loci examined. This was higher than that found among populations of other *Peromyscus* species, but the loci sampled included eight non-specific esterases, which typically exhibit higher polymorphisms. Margaret Smith (1979), working with James Patton at U.C.-Berkeley, examined 13 presumptive loci in *P. californicus*. Variants at four of these loci sharply differentiated northern from southern populations, generally assignable to the subspecies *P. c. californicus* and *P. c. insignis*, respectively. At the University of Colorado - Denver, Ramone Baccus and Jim Joule, along with W.J. Kimberling, (1980) found nine of 19 presumptive loci were sufficiently polymorphic to test for linkage using Morton's lod-score method. They also tested the data using selection component analysis (Nadeau and Baccus, 1981). In addition, spatial-temporal changes in allelic frequencies were detected during this study (Massey and Joule, 1981). Ramone subsequently became a technician at Mike Smith's SREL lab before advancing to Ph.D. work with William Lidicker at Berkeley. Phyllis Price and Mike Kennedy (1980), at Memphis State University, sampled *P. leucopus* and *P. gossypinus* at 36 sites from Oklahoma to eastern Tennessee, testing 14 loci, of which 9 were polymorphic within or among sites. *P. gossypinus* was less variable than was *P. leucopus*. They found that mean heterozygosities were remarkably variable over the study area.

By the late 1970s Selander had moved to the University of Rochester and away from his involvement with *Peromyscus*. Earl Zimmerman gradually abandoned his *Peromyscus* emphasis to work with population genetics of gophers (but in recent years has been again investigating the *P. boylii* group applying mtDNA analysis). In 1973 Mike Smith was appointed Director of SREL, replacing Frank Golley. Mike's major research thrust shifted to allelic frequency changes in white-tail deer, a continuing study now with more than 20 years of accumulated data. Furthermore, Mike developed an allergy to *Peromyscus*, thus, his efforts with these rodents

diminished. However, two individuals, Avise at Georgia, and Kilpatrick, who joined the faculty at The University of Vermont in 1974, continued to work with the genus. John Avise was first author (1979) of the final paper (VII) in the "Biochemical polymorphism and systematics in the genus *Peromyscus*" series. This paper treated populations of the *P. maniculatus* and *P. truei* species groups. The surprise in this paper was the remarkable uniformity of allozyme polymorphism among *P. maniculatus* populations. Six of 21 loci scored were highly polymorphic. Eighteen widespread populations of this species shared similar alleles at both monomorphic and polymorphic loci, suggestive of a late Pleistocene dispersal from a smaller founding population. Levels of heterozygosity were high (5.5 - 12.4%) in all populations, consistent with Loudenslager's (1978) observations on a smaller scale in Wyoming. F_{ST} values for *P. maniculatus* were essentially the same as those between house mouse populations on different farms in Texas studied earlier by Selander. A phenogram generated from the data indicated that *P. melanotis* was specifically distinct from the deer mouse. In the late 1970s Avise, along with his graduate student, Charles "Chip" Aquadro, investigated "hidden" polymophisms, amylase variation and, in collaboration with Robert Lansman and others, began to explore mtDNA restriction site variation in *Peromyscus* - but that's another story for another day.

At Vermont, Bill Kilpatrick and his graduate students, Aquadro, Paul Rennert, Jack Sullivan and Darrin Werbitsky, continued to explore *Peromyscus* protein polymorphism well into the 1980s, concentrating on *P. boylii* of Mexico and other mesoamerican species. Bill (1984) examined biochemical relationships of *P. attwateri* relative to *P. boylii*, concluding that these these two taxa been separated for 170,000 years. Rennert and Kilpatrick (1986, 1987) found genic differentiation among several forms of nominal *P. boylii*, which generally corresponded to populations also differentiated chromosomally. Three subdivisions, possibly species, within the framework of *P. boylii*, were "*levipes*", "*rowleyi*" and "*beatae*". Sullivan extended the electrophoretic survey to include additional taxa of the *P. boylii* group, concluding that the group is monophyletic, with the possible exception of *P. pectoralis*, which associated more closely with *P. eremicus* using Rogers's distance estimate (Sullivan, Kilpatrick and Rennert, 1991). Sullivan and Kilpatrick (1991) also surveyed the *P. aztecus* assemblage, and Werbitsky and Kilpatrick (1987) analyzed protein variation in *Megadontomys*. The latter study indicated that *M. thomasi* is differentiated from *Peromyscus* (*sensu stricto*) species used in the genetic distance measures. By the end of the 1980s, Bill's interest had turned to DNA-DNA hybridization and DNA sequencing as systematics methodologies.

Various others (*e.g.* Krohne and Baccus, 1985; Mewaldt and Jenkins, 1986; Tolliver *et al.*, 1986; Calhoun *et al.*, 1988; Sugg *et al.*, 1990; Schnake-Greene *et al.*, 1990; Janecek, 1990; Calhoun and Greenbaum, 1991; Rogers and Engstrom, 1992) continued to run starch gel electrophoresis of *Peromyscus* allozymes during the mid-1980s. But by then, as molecular approaches to population genetics and systematics became practical, allozyme research became passe. Agarose was in and starch was out. Another bandwagon had left the gate.

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HANTAVIRUS AND *PEROMYSCUS*:

AN EMERGING PARADIGM

In 1993 news of an outbreak of a severe, often fatal, pneumonia-like human disease in the U.S. southwest spread alarm within epidemiological community, as well as among the general public, that a dangerous "new" pathogenic organism had appeared, or worse yet, had been inadvertantly or even deliberately released, in North America. Within weeks CDC had identified the causative agent as a previously unknown hantavirus carried by rodents, especially deer mice. The illness became known as HPS (hantaviral pulmonary syndrome) to distinguish it from diseases with renal complications caused by other hantaviruses. It was widely reported in the press that this was the first occurrence of hantaviral disease in humans in North America. Some epidemiologists, particularly James Childs of CDC, formerly of Johns Hopkins School of Public Health, and Richard Yanagihara of NIH, were aware that rats (*Rattus*), voles and other rodents in North America carried hantaviruses, although the Four Corners type differed genetically.

In the interim since the initial HPS outbreak an immense amount of information has accumulated. Included are field studies of rodent populations, tests on long-frozen tissue samples, re-examination of cases among persons, both living and deceased, who had exhibited HPS-like symptoms in the past, identification of various strains of hantavirus based on both serology and nucleic acid sequences, tests on hundreds of animals from both wild and captive populations of deer mice and other native rodents, and tests on mammalogists, exterminators and others who have regular contact with rodents. Major organizations conducting this research are CDC, NIH, USAMRIID (Army) and the University of New Mexico. We are aware of more than 40 papers published during the past year and a half on American hantaviruses. From this research a consensus appears to be in the making. As we perceive it, the following are some of the premises and conclusions:

Hantaviruses are endemic in low frequency in many rodent populations. Each hantavirus has a primary rodent host, and different myomorphic rodent taxa harbor different hantavirus varieties (species) and serve as reservoirs for particular viral strains or species. Brian Hjelle and colleagues (New Mexico School of Medicine) have evidence that hantaviruses co-evolve with their primary muroid host at the level of genera and families based on similarity of nucleic acid sequence branching pattern in the viruses compared with that of host phylogenies. Sergey Morzunov (CDC) is finding that the same correspondence extends to the species, and even subspecies, level of *Peromyscus*. Hence, hantaviruses did not recently invade *Peromyscus* as was the popular initial impression, but have likely been present in deer mice and other native rodents all along.

Primary hosts apparently are unaffected by the their indigenous virus types. Hantaviruses may infect humans as a secondary host and produce disease. Severity and symptoms of disease in humans depends on the species of hantavirus contracted. The virus elicits a hyper-immunoresponse in humans which initiates a cascade of events resulting in HPS. Healthy young individuals are as likely, or more likely, at risk than children or elderly persons.

Under normal circumstances wild rodent populations show a low incidence of hantaviral infection as detected by serology. However, as populations become more dense, when food is exceptionally abundant, as was the case the the Four Corners outbreak, and rodent-to-rodent contact is increased, the incidence of infected rodents may dramatically increase. Under these circumstances, where human contact with rodents occurs, the probability of human infection also increases. Rodent-to-rodent transmission is likely to be from bites sustained during aggressive encounters. Transmission among rodents is less likely to occur from casual association. Prepuberal rodents generally test negative. Transmission to humans is likely from inhalation of viral particles from rodent feces or urine.

What are the risks, especially to mammalogists? Probably no more or less than before 1993. But with the knowledge, appropriate precautions are in order.

PEROMYSCUS STOCK CENTER

What is the Stock Center? The deer mouse colony at the University of South Carolina has been designated a genetic stock center under a grant from the Special Projects Program of the National Science Foundation. The major function of the Stock Center is to provide genetically characterized types of *Peromyscus* in limited quantities to scientific investigators. Continuation of the center is dependent upon significant external utilization, therefore potential **users are encouraged to take advantage of this resource.** Sufficient animals of the mutant types generally can be provided to initiate a breeding stock. Somewhat larger numbers, up to about 50 animals, can be provided from the wild-type stocks.

A user fee of **$10 per animal** is charged and the user assumes the cost of air shipment. Animals lost in transit are replaced without charge. Tissues, blood, skins, *etc.* can also be supplied at a modest fee. Arrangements for special orders will be negotiated. Write or call for details.

Stocks Available in the Peromyscus Stock Center:

WILD TYPES	ORIGIN
P. maniculatus bairdii (BW Stock)	Closed colony bred in captivity since 1948. Descended from 40 ancestors wild-caught near Ann Arbor MI
P. polionotus subgriseus (PO Stock)	Closed colony since 1952. Derived from 21 ancestors wild-caught in Ocala Nat'l. Forest FL. High inbreeding coefficient.
P. polionotus leucocephalus (LS Stock)	Derived from beachmice wild-caught on Santa Rosa I., FL. and bred by R. Lacy. Seventh to tenth generation in captivity.
P. leucopus (LL Stock)	Derived from 38 wild ancestors captured between 1982 and 85 near Linville NC. Eighteenth to twenty-fourth generation in captivity.
P. californicus insignis (IS Stock)	Derived from about 60 ancestors collected between 1979 and 87 in Santa Monica Mts. CA. Tenth to twelfth generation in captivity.
P. aztecus	Derived from animals collected on Sierra Chincua, Michoacan, Mexico in 1986 Seventh to tenth generation in captivity.
P. maniculatus X *P. polionotus* F_1 Hybrids	Sometimes available.

MUTATIONS AVAILABLE FROM THE STOCK CENTER[1]

Coat Colors	**ORIGINAL SOURCE**
Albino *c/c*	Sumner's albino deer mice (Sumner, 1922)
Ashy *ahy/ahy*	Wild-caught in Oregon ~ 1960 (Teed *et al.*, 1990)
Black (Non-agouti) *a/a*	Horner's black mutant (Horner *et al.*, 1980)
Blonde *bln/bln*	Mich. State U. colony (Pratt and Robbins, 1982)
[2]Brown *b/b*	Huestis stocks (Huestis and Barto, 1934)
Dominant spotting *S/+*	Wild caught in Illinois (Feldman, 1936)
Golden nugget b^{gn}/b^{gn} [in *P. leucopus*]	Wild caught in Massachusetts (Horner and Dawson, 1993)
Gray *g/g*	Natural polymorphism From Dice stocks (Dice, 1933)
Ivory *i/i*	Wild caught in Oregon (Huestis, 1938)
[3]Pink-eyed dilution *p/p*	Sumner's "pallid" deer mice (Sumner, 1917)
Platinum *plt/plt*	Barto stock at U. Mich. (Dodson *et al.*, 1987)
[2]Silver *si/si*	Huestis stock (Huestis and Barto, 1934)
Tan streak *tns/tns*	Clemson U. stock from N.C. (Wang *et al.* 1993)
Variable white *Vw/+*	Michigan State U. colony (Cowling *et al.* 1994)
White-belly non-agouti a^{w}/a^{w}	Egoscue's "non-agouti" (Egoscue, 1971)
Wide-band agouti A^{Nb}/a	Natural polymorphism. U. Michigan stock (McIntosh, 1954)
Yellow *y/y*	Sumner's original mutant (Sumner, 1917)

MUTATIONS AVAILABLE FROM THE STOCK CENTER[1] (continued)

Other Mutations and Variants	**ORIGIN**
Alcohol dehydrogenase negative *Adh*^{o}/*Adh*^{o}	South Carolina BW stock (Felder, 1975)
Alcohol dehydrogenase positive *Adh*^{f}/*Adh*^{f}	South Carolina BW stock (Felder, 1975)
[4]Boggler *bg/bg*	Blair's *P. m. blandus* stock (Barto, 1955)
Cataract-webbed *cwb/cwb*	From Huestis stocks. (Anderson and Burns, 1979)
[4]Epilepsy *ep/ep*	U. Michigan *artemisiae* stock (Dice, 1935)
[3]Flexed-tail *f/f*	Probably derived from Huestis flexed-tail (Huestis and Barto, 1936)
Hairless-1 *hr-1/hr-1*	Sumner's hairless mutant Sumner (1924)
Hairless-2 *hr-2/hr-2*	Egoscue's hairless mutant (Egoscue, 1962)
[4]Juvenile ataxia *ja/ja*	U. Michigan stock (Van Ooteghem, 1983)

Enzyme variants. Wild type stocks given above provide a reservoir for several enzyme and other protein variants. See Dawson *et al.* (1983). For origin references see *PN* #18, pp.25-26.

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[1]Unless otherwise noted, mutations are in *P. maniculatus*.

[2]Available only as silver/brown double recessive.

[3]Available only as pink-eye dilution/flexed-tail double recessive.

[4]Available from Behavior Mutant Center

Note: Some of the mutations are immediately available only in combination with others. For example, silver and brown are maintained as a single "silver-brown" double recessive stock. Write the Stock Center or call (803) 777-3107 for details.

OTHER RESOURCES OF THE *PEROMYSCUS* GENETIC STOCK CENTER:

Limited numbers of other stocks, species, mutants, inbreds and variants are on hand, or under development, but are not currently available for distribution. For additional information or details about any of these mutants or stocks contact: Janet Crossland, Colony Manager, Peromyscus Stock Center, (803) 777-3107.

Preserved or frozen specimens of types given above.

Tissues, whole blood or serum of types given above.

Flat skins of mutant coat colors or wild-type any of the species above.

Reference library of more than 2400 reprints of research articles and reports on *Peromyscus*.
Copies can be xeroxed and mailed.

Materials are now available through the *Peromyscus* Molecular Bank of the Stock Center. Allow two weeks for delivery. Included is purified DNA or frozen tissues from any of the stocks listed above. Several genomic and cDNA libraries and a variety of molecular probes are available.
(See next page)

PLEASE CALL WITH INQUIRIES.

Peromyscus Genetic Stock Center
University of South Carolina
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Materials on Deposit in the *Peromyscus* Molecular Bank

Accession Number	Item	Description	Species	Donor	Location[1]
Probes and Clones:					
Pr-01	LINE1	pDK62	*P. maniculatus*	D. Kass	C
Pr-02	LINE1	pDK55	*P. maniculatus*	D. Kass	C
Pr-03	ADH1	pADH F72	*P. maniculatus*	M. Felder	B
Pr-04[2]	Mys		*P. leucopus*	(Requested)	
Pr-05[2]	SAT		*P. leucopus*	(Requested)	
Pr-06	6PGD	pB5 clones	*P. californicus*	S. Hoffman	A
Pr-07	MHC *Pele*I	38dp2	*P. leucopus*	M. Crew	A
Pr-08	MHC *Pele*I	52ap6	*P. leucopus*	M. Crew	A
Pr-09	MHC *Pele*I	40Bgl	*P. leucopus*	M. Crew	A
Pr-10	MHC *Pele*I	53Pv1	*P. leucopus*	M. Crew	A
Pr-11	MHC *Pele*I	37B2	*P. leucopus*	M. Crew	A
Pr-12	MHC *Pele*I	37B4	*P. leucopus*	M. Crew	A
Pr-13	MHC *Pele*II	α3E23	*P. leucopus*	M. Crew	A
Pr-14	MHC *Pele*III	17E2	*P. leucopus*	M. Crew	A
Pr-15	MHC *Pema*I	pr44	*P. maniculatus*	M. Crew	A
Libraries:					
Lb-01	lambda genomic	liver (ADH+)	*P. maniculatus*	M. Felder	B
Lb-02	lambda cDNA	liver	*P. maniculatus*	M. Felder	B
Lb-03	lambda genomic	testis	*P. leucopus*	M. Crew	A
Lb-04	cosmid genomic	testis	*P. leucopus*	R. Baker	A
Lb-05	lambda genomic	liver	*P. californicus*	S. Hoffman	A
Frozen Tissue for DNA:					
S-01	bairdii (BW)	liver, other[3]	*P. maniculatus*	Stk. Ctr.	A
S-02	subgriseus (PO)	liver, other	*P. polionotus*	Stk. Ctr.	A
S-03	leucopus (LL)	liver, other	*P. leucopus*	Stk. Ctr.	A
S-04	wild-caught SC	liver, other	*P. gossypinus*		A
S-05	aztecus	liver, other	*P. aztecus*	J. Glendinning	A
S-06	insignis (IS)	liver, other	*P. californicus*	S. Hoffman	A
S-07	inbred PmH1A	liver, other	*P. maniculatus*	Jackson Lab	A
S-08	inbred PmH8	liver, other	*P. maniculatus*	Jackson Lab	A

[1]Location code: **A** = USoCar SAI 01; **B** = USoCar CLS 603; **C** = USoCar CLS 707

[2]Not currently available.

[3]kidney, spleen, testis, carcass.

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POPULATIONS OF *PEROMYSCUS PSEUDOCRINITUS* IN CORONADOS ISLAND, GULF OF CALIFORNIA, MEXICO.

In this work, we visited Coronados Island to estimate endemic rodent populations, as a part of the global research on fauna, that is being carried out in the Islands of the Gulf of California by the scientific staff of the Centro de Investigaciones Biologicas del Noroeste.

Coronados is a volcanic island located at coordinates 26°06'N and 111°18'W, with an area estimated in 8.5 km^2. The fauna in this island is characterized by three endemic rodent species, *Peromyscus pseudocrinitus*, *Chaetodipus spinatus pullus* and *Neotoma bunkeri*. Because of their limited distribution, all these species are under a risk of extinction in the island. In this sense, and due to the presence of a domestic cat (*Felis catus*) population in the island, the survival of the rodent species is being threatened. In accordance, in other islands all over the world, several researchers have found that introduced domestic cat is a very dangerous and effective predator for resident species (Veitch, 1980; Ebenhard, 1988; Arnaud, 1993; Seabrook, 1990). Nevertheless, there is a lack of studies related to ecological implications and the current status of endangered rodent populations.

For estimating rodent populations in Coronados, we visited this island from September 6th to 10th, 1995. The rodents were caught alive with Sherman type traps, located in nine sites in different habitats within the island: xerophylous shrub in a coastal plateau with calcareous soil, halophyte vegetation, beach vegetation and stabilized dunes, and xerophylous shrub established in intemperized volcanic rocky soils type I and II. Two 'one-hectare' quadrants and seven transects (100, 200 or 400 m) were sampled, for a total area of 201,200 m^2.

The biggest number of trapped individuals corresponded to *Chaetodipus spinatus pullus*; on the other hand, *Peromyscus pseudocrinitus* showed a very low population density, given by only twelve individuals collected in the 908 working traps established in every kind of vegetation.

Cat feces were collected from the different habitats in the island; we found through microscope analysis that *P. pseudocrinitus* is part of their food composition. After studying the available evidences, we concluded that *P. pseudocrinitus* population is very low, despite its wide distribution along the island. We suggest a prompt eradication of the introduced cat population in order to guarantee the survival of this endemic species in the Coronados Island.

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* * *

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The Pennsylvania Bureau of Forestry has recently adopted (1991) a new forest management practice called Even-Aged Reproduction (EAR) with Reservation Guidelines. Essentially, these guidelines call for the retention of an average basal area of between 10-20 square feet over the entire treatment area and a minimum of five trees per acre. A variety of tree species are retained to enhance plant species diversity.

The purpose of our study (which was initiated in 1995) was to examine wildlife biodiversity associated with six of these stands. For each site, we also established a reference area in a contiguous, uncut forest. While censusing small mammals, *Peromyscus leucopus* was by far the most common species found. In the sites, an average of 16.25 mice were caught per trap night, and in the reference, 17 were caught per trap night. These preliminary results indicate that this type of management plan does not have a severe impact on the *P. leucopus* population.

* * *

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CERTAIN ODORS HAVE LITTLE EFFECT ON PREGNANCY MAINTENANCE IN DEER MICE, *PEROMYSCUS MANICULATUS BAIRDI*

I wish to summarize several studies that have generated negative results and which I plan neither to publish nor to extend. There is good evidence that the post-mating environment can affect pregnancy maintenance in mated female rodents (*e.g.*, de Cantanzaro, D., & MacNiven, E. 1992. Neurosci. Biobehav. Rev. 16:43-53; Dewsbury, D. A. 1995. Physiol. Behav. 57:827-829). In this work we explored the effects of several treatments on deer mice.

In a first study 19 parous females were mated with stud males in two tests each in a counterbalanced design. After mating in cycling estrus for three ejaculatory series per test in the male's home cage, females were returned to their cages with either their own bedding or bedding from the cage of the male with which they had just mated. Whereas 68% of the females delivered litters after placement on their own bedding, 47% delivered with male bedding; the difference was not significant.

A second experiment was designed to determine whether odors from other females might affect pregnancy maintenance (see Huck, U. W., Bracken, A. C., & Lisk, R. D. 1983. Behav. Neur. Biol. 38:190-193). After mating as in Experiment 1, females were either returned to their home cage or placed in a soiled cage from a different, unrelated female. In a between-subjects design, 5 of 7 females delivered litters in each condition. There was no suggestion of an effect.

A third study was conducted to test effects of odors from an alien species, prairie voles (*Microtus ochrogaster*). Seventeen female deer mice, virgin at the start of the study, received two tests in which they were allowed to copulate for 2 h after the first intromission. There was a bedding change every third day after mating: either fresh bedding or bedding from group-housed prairie voles was introduced. Thirteen females delivered in the vole bedding condition; 12 in the control condition. There was no detectable effect of the manipulation.

Although some treatments can cause a pregnancy block in deer mice (Dewsbury, D. A. 1982. Behav. Ecol. Sociobiol. 11:37-42) and these studies should be extended with altered treatment parameters, these results suggest that pregnancy maintenance in deer mice is less sensitive to odors than in other species.

(continued)

Donald A. DEWSBURY (continued)

VAGINAL SMEARS DO NOT AFFECT PREGNANCY MAINTENANCE IN DEER MICE, *PEROMYSCUS MANICULATUS BAIRDI*

In most studies of pregnancy conducted over a number of years in this laboratory, vaginal smears were used to determine the period of estrus in female deer mice and were continued after mating so that pseudopregnancies could be differentiated from tests with no alteration of the female cycle. In this study we examined the effect of this procedure to determine whether the very process of taking vaginal smears might affect pregnancy maintenance.

Virgin females were caged individually and vaginal smears were taken with a thin wire loop each morning. They were mated with stud males in the afternoon of proestrus in two tests each in a repeated-measures design. After one test smears were continued until either delivery of a litter or it became clear that the female was not pregnant. Smears were discontinued after the other test for each female.

In Experiment 1, 10 females were permitted to mate for one ejaculatory series per test. Three litters were born in the "smear condition;" one was born in the "no smear" condition. The difference was not significant.

In Experiment 2, 10 other females were studied with two ejaculatory series permitted per test. Eight of the 10 delivered in the "smear condition;" 10 of 10 in the "no smear" condition.

In Experiment 3, 10 other females were studied with three ejaculatory series per test. Seven females delivered in each condition.

Although these data confirm earlier reports of a relationship between the amount of copulation and pregnancy initiation, at least beyond one series (Dewsbury, D. A. 1979. J. Comp. Physiol. Psychol. 93:178-188), they suggest no effect of the vaginal smear procedure.

Reports to be continued in Peromyscus Newsletter #21.

* * *

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PLEIOTROPIC EFFECTS OF THE AGOUTI COAT-COLOR LOCUS IN *PEROMYSCUS*

I examined the effects of stress on reproductive output of agouti and extreme nonagouti *Peromyscus*. The stress used was shipping the animals overseas. In February and again in June, 24 pairs of deer mice (12 of each color morph) were shipped to the UK and paired upon arrival. A control set of 24 pairs was paired in the US at the same time (total 96 pairs). Reproductive output (litter size, time from pairing to birth, proportion of pairs having litters, interbirth interval) was monitored for 4 months post shipping. Shipping strongly reduced the fecundity of both colormorphs. Within 40 days of pairing, 46% of both control colormorphs had littered whereas only 17% of the agouti and 25% of the nonagouti stressed pairs produced offspring. After 100 days, 63% of the agouti controls and 71% of the nonagouti controls had litters compared with 42% of the stressed agouti pairs and 33% of the stressed nonagouti mice. Possibly, stress had a stronger acute effect on agoutis (8% fewer litters) and a longer, more chronic effect on nonagoutis. Shipping had no effect on fertility but colormorph did. Litter size was similar in both stressed and unstressed pairs, but was smaller for agoutis (3.4 vs 4.3).

* * *

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PHYLOGENETIC STUDY OF HANTAVIRUS/RODENT HOST RELATIONSHIPS AND THE COEVOLUTION

Recent epidemics of hantavirus-associated illness and rapidly expanding numbers of newly identified hantaviruses, have increased interest in the determination of the public health threat posed by these viruses, and their ecology and natural evolution. Each of the known hantaviruses is primarily associated with a single species of rodent. All available data suggest a long term coevolution of hantaviruses with their specific rodent hosts. In general, genetic and serologic relationships of different hantavirus isolates correlate with their geographic distribution although some consistent exceptions are observed.

To better understand the ecology, transmission, and mechanisms of coevolution of hantaviruses and their rodent hosts, an extensive study of the genetic relationship of rodent hosts of known hantaviruses has been initiated. Generic primers were designed based on known rodent mitochondrial DNA sequences, and a 2 Kb fragment of mitochondrial DNA of different rodent species, including the 3′ part of the cytochrome B gene and the replication control region ("D-loop region"), was successfully amplified and sequenced. A 400 nucleotide fragment of the 3′ coding part of the cytochrome B gene was chosen for analysis of the relationship of distant rodent species, and a variable 330 nucleotide fragment of the control region was used for the analysis of intraspecies variability. Such DNA fragments were amplified from numerous hantavirus PCR-positive *Peromyscus* rodents, and phylogenetic analyses and virus-host comparisons are currently in progress.

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LARGE *PEROMYSCUS GOSSYPINUS* FROM THE DISMAL SWAMP OF VIRGINIA, THE FIRST SPECIMENS SINCE DICE'S COLLECTIONS IN THE 1930s.

On 12 March, 1994, Victor Townsend, an undergraduate student working on an honors project with me and our herpetologist (Alan Savitzky) collected three large *Peromyscus* in the Northwest River Park (City of Chesapeake, VA) while assessing the foods of the local canebrake rattlesnakes and copperheads. (The Northwest River is one of the streams draining the Dismal Swamp waters to the southeast, so this watershed really is an extension of the Dismal Swamp.) I thought the *Peromyscus* might be *P. gossypinus*, which haven't been collected in the Dismal Swamp region since Lee Dice and Don Hayne trapped some specimens for lab studies in the 1930s. So, I prepared the specimens as skins and skulls and sent them to Charles O. Handley, Jr. at the NMNH. A year later, after the skulls made the trip through the dermestid colony, Charles has related to me that these are indeed *Peromyscus gossypinus*, and in fact are the largest specimens of this species that he has seen.

The specimens were collected in Museum Special traps, and had the following dimensions:

RKR 5385 male 192-88-24-18 = 35 g
RKR 5386 female 205-97-25-18 = 34 g
RKR 5387 male 199-80-23-18 = 33 g

All are now in the collection of the NMNH, but I do not know the accession numbers.

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INTERACTIONS BETWEEN DEER MICE AND GRASSHOPPER MICE ON NORTHERN SHORTGRASS STEPPE

Since 1992, we have conducted field studies of various aspects of habitat use and community structure of rodents on the shortgrass steppe in north-central Colorado. Deer mice (*Peromyscus maniculatus*) are relatively common on the site and we recently completed two studies to examine interactions between deer mice and northern grasshopper mice (*Onychomys leucogaster*). Grasshopper mice reportedly consume other rodents, including deer mice, and although the frequency and significance of predation have not been established, we predicted that deer mice might shift habitat use to avoid the larger grasshopper mice. Both species consume arthropods during spring and early summer, so competitive interactions are also possible.

In 1994, we removed grasshopper mice from four of eight sites and recorded changes in the abundance, microhabitat use, and diet of deer mice in response to removals. Deer mice did not colonize removal sites, but instead declined markedly in number on control sites in association with an increase in grasshopper mice. Population-level responses, however, were complicated by an area-wide decline in deer-mouse numbers. Furthermore, we did not detect significant shifts in the use of shrub microhabitats on removal sites; rather, on control sites deer mice increased their use of shrubs, particularly when grasshopper-mouse numbers were high. Deer mice may have moved farther into shrubs to avoid grasshopper mice, which show no apparent affinity for shrubs. Because we also observed no changes in the diet of deer mice, we attributed shifts in habitat use and abundance to aggressive interference or predation rather than competition.

Because of the widespread use of olfactory communication in rodents, and because grasshopper mice have a strong musky odor, we predicted that deer mice would use olfactory cues to detect and avoid grasshopper mice. In a series of trap-response experiments, we compared the captures of deer mice in traps containing grasshopper-mouse odors to those in traps containing harvest mouse odors and in clean traps. Contrary to our predictions, deer mice did not avoid grasshopper-mouse odors, regardless of the sex of respondents, or whether or not mice had prior exposure to grasshopper mice. Our results corroborate the observations of Elizabeth Harper and her co-workers in an earlier issue of the PEROMYSCUS NEWSLETTER (#19). In a manuscript submitted to Canadian Journal of Zoology, we suggest that the apparent indifference of deer mice to heterospecific olfactory cues may reflect differences in population biology and life history traits between deer mice and rodents that generally avoid predator odors.

In 1994, the NSF Shortgrass Steppe Long-Term Ecological Research (LTER) project began regular sampling of rodent populations on our study site, the Central Plains Experimental Range. Three upland prairie and three saltbush (*Atriplex canescens*) trapping webs (3.14 ha) are trapped in late-spring and late-summer. These studies are part of long-term monitoring programs on the site and will useful for comparative studies among sites in the LTER network and for tracking changes in populations of deer mice and other rodents over time.

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STUDIES OF WILD *PEROMYSCUS LEUCOPUS NOVEBORACENSIS* POPULATIONS

Since 1983, I have been studying natural populations of white-footed mice living on an 11 ha grid. I have shown (1993) reproduction significantly declines in May, June and July of each year at drastically different numerical levels. Papers currently being submitted for publication explore the influence of supplemental food and density manipulation on this mid-summer reproductive curtailment. Reproductive recovery of inhibited animals has also been explored in the laboratory and in a semi-natural environment.

Kin Recognition Experiments

Recent work with Anne Smith has examined whether kin are recognized and more attractive in a choice apparatus to white-footed mice than non-relatives. This study is being readied for publication and reveals considerable variation from previous studies of this phenomenon.

Pregnancy Block in *Peromyscus maniculatus bairdii*

Questions concerning the adaptive significance of the pregnancy block (Bruce effect) phenomenon are being explored by Tavis Sipe in my laboratory. The use of the Video-mex equipment has made it possible to measure the proximity response of recently inseminated females to choices involving the stud male or stranger male and the influences of such choices on pregnancy.

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