

# PEROMYSCUS NEWSLETTER

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NUMBER FIVE

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MARCH 1988



Cover sketch\* by  
David I. Rasmussen,  
Arizona State University

\*From Biology of Peromyscus,  
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1968.

ABOUT THIS ISSUE.....

Peromyscus Newsletter #5 contains the 1988 updated lists of genetic loci for the deer mouse (P. maniculatus). Table I, in four sections, lists the genetic loci demonstrated by formal mendelian analysis. Table II lists presumed loci identified from protein variants in natural populations. These tables reflect a continuing effort to make the genetic symbols and nomenclature for Peromyscus consistent with that of the laboratory mouse, particularly where homology is evident. Also included in this issue for the first time is an extensive table of published interspecific hybridization attempts in Peromyscus. References cited in the tables are listed in Bruce Buttler's "Bibliography of Peromyscus (Rodentia): Genetics".

Several announcements are of interest. Particularly noteworthy is the announcement of the forthcoming volume "Advances in the Study of Peromyscus (Rodentia)" edited by Gordon Kirkland and Jim Layne and to be published by Texas Tech University (See p. 6, this issue). This volume is an outgrowth of a symposium held at the Fourth International Theriological Congress in 1985. All peromyscologists will be looking forward to this book.

Our "Peromyscus Pioneer" biographical sketch for PN #5 treats W. Frank Blair. We are indebted to many individuals for furnishing information, publications and anecdotes. In preparation of this sketch we relied heavily upon an obituary prepared by Dr. Clark Hubbs of the University of Texas. Dr. Hubbs was a long-time friend of Frank Blair and we appreciate immensely the biographical material he gave us. Elizabeth Horner and William McIntosh provided us reprints of some of Blair's early papers. We corresponded or spoke with several others who knew Blair and from these insights feel we have a greater appreciation than ever for this remarkable man. We recognize that Frank Blair was probably best known for his work with amphibians which was conducted during his 36 years on the University of Texas faculty; however, in our sketch we have stressed his earlier and, perhaps, equally significant, contributions to the biology of Peromyscus. Those who want a fuller discussion of Blair's career should consult Hubbs' account (Copeia, 1985:529-531).

**A REMINDER** that PEROMYSCUS NEWSLETTER is an informal publication intended to report work-in-progress, preliminary results and other information of interest to those working with the genus. Therefore, **material reported in PEROMYSCUS NEWSLETTER should not be cited in publication except with permission of the contributor.** Entries are given verbatim without editing except for format. Occasional typographical errors may occur and we beg your forbearance. Please continue to send reports of your research activity. PN #6 is scheduled for September. The entries should reach us by 15 August 1988.

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## NEWS AND COMMENT

Our request in PN #4 for a donation of a copy of McCabe and Blanchard's Three Species of Peromyscus for our Deer Mouse Center reference library met with success. Elizabeth Horner of Smith College kindly gave us a hard bound copy which is greatly appreciated and William McIntosh also donated his copy. In addition Bill McIntosh kindly contributed early issues of Journal of Mammalogy, Evolution, Journal of Heredity and other journals and books relevant to the Peromyscus.

Van T. Harris recently graciously donated some of the now-classic works of neodarwinism by Dobzhansky, Mayr, Huxley, Rensch and others.

Elizabeth Horner also gave the Center a series of study skins of P. maniculatus and P. leucopus collected in the 1940's.

These items enrich the Peromyscus Stock Center reference collections and enhance its research potential. They are greatly appreciated. THANKS !!!

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BACK ISSUES OF PEROMYSCUS NEWSLETTER. We have had numerous requests for the earlier issues of PN. Unfortunately, our supply has been exhausted of all but #4. We have a few copies remaining of that (Sept. '87) issue. There are currently about 275 names on the mailing list and we run 300 copies, so the supply of back issues doesn't last long. Remember, we are an informal desk-top, xerox machine operation!

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John A. Sealander of the University of Arkansas, Fayetteville, will retire in May. For many years he used Peromyscus to study metabolic and hematological changes in response to different environmental conditions.

\*\*\*\*\*

James Jaeger of the University of Wisconsin informs us that the stock of Peromyscus Judy Paul referred to in PN #1 has been discontinued. However, he is keeping stocks of P. leucopus and P. maniculatus from Wisconsin, Wyoming and Canada. Jaeger also has a small number of black (non-agouti) deer mice. He is willing to provide persons doing genetics with this stock. He is having problems maintaining it because of space limitations.

xxxxxxxxxxxxxxxx



We have been informed that Garret Clough of Newburgh NY died May 22, 1987. Clough investigated Peromyscus and other small mammals in managed forests.

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Harold Egoscue continues his studies of factors involved in the ecology of Peromyscus fleas in the Great Basin. The distribution of some species of fleas is independent of the primary hosts. He is seeking to identify ecological factors involved.

+++++

Bruce Cushing has returned from Hawaii and expects to return to work with Peromyscus in the near future. Bruce and Nancy are proud parents of a son, Wade, born in December.

#### A N N O U N C E M E N T S

DISPERSAL OF PEROMYSCUS (RODENTIA): A BIBLIOGRAPHY, the third in Bruce Buttler's series of bibliographies on the genus will soon be available free of charge. Copies may be obtained from him % Division of Natural and Physical Sciences, Canadian Union College, Box 430, College Heights, Alberta T0C 0Z0, Canada.

+ + + + +

A highly specific double antibody homologous radioimmunoassay kit for measuring prolactin in Peromyscus is available from Dr. Frank Talamantes, Thimann Laboratories, University of California, Santa Cruz, California 95064.

Information about this RIA can be obtained from the following publications:

1. Colosi, P., Bewley, T.A. and Talamantes, F. 1983. Isolation, purification and characterization of deer mouse (Peromyscus maniculatus bairdii) prolactin. Arch. Biochem. Biophys. 222:621-627.
2. Marr, G.A., Colosi, P., Desjardins, C. and Talamantes, F. 1983. Development and characterization of a homologous radioimmunoassay for deer mouse (Peromyscus maniculatus bairdii) prolactin. Life Sciences 33:2305-2309.

\* \* \* \* \*

PEROMYSCUS VOLUME IN PRESS. "Advances in the Study of Peromyscus (Rodentia)" edited by Gordon L. Kirkland, Jr. and James N. Layne is scheduled for publication by Texas Tech University during this coming summer. The volume is an outgrowth and expansion of a symposium, "Biology of Peromyscus (Rodentia):1968-1985," presented at the Fourth International Theriological Congress in Edmonton, Canada, in August 1985. The objective of the book is to review the major advances in knowledge of Peromyscus biology in the 20 years that have elapsed since the publication of King's "Biology of Peromyscus," with emphasis on five areas that have been particularly dynamic. The topics and authors include "Systematics and Evolution" by Michael D. Carleton, "Adaptive Physiology" by Richard E. MacMillen and Theodore Garland, Jr., "Reproduction and Development" by John S. Millar, "Population Biology" by Donald W. Kaufman and Glennis A. Kaufman, and "Social Behavior" by Jerry O. Wolff. The final chapter, "Peromyscus and Apodemus: Patterns of Similarity in Ecological Equivalents" by W. I. Montgomery provides a comprehensive comparative review of the ecophysiology, reproduction, population dynamics, trophic relationships, and other aspects of the biology of the New World genus Peromyscus and the Old-World genus Apodemus. Although these genera often have been regarded as ecological equivalents, the extent to which this is true has not previously been critically examined. Individuals interested in purchasing this volume should correspond with Carole J. Young, Editor, Texas Tech University Press, Box 4139, Lubbock, TX 79409 (Phone 806/742-2417).



## 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 Biological Resources 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 \$5 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 charge. Write or call for details.

### Stocks Available in the Center:

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WILD TYPES	ORIGIN
<i>P. maniculatus bairdii</i> (BW Stock)	Closed colony bred in captivity since 1948. Descended from 40 ancestors wild-caught near Ann Arbor MI
<i>P. polionotus subgriseus</i> (PO Stock)	Closed colony since 1952. Derived from 21 ancestors wild-caught in Ocala Nat'l. Forest FL. High inbreeding coefficient.
<i>P. leucopus</i> (LL Stock)	Derived from 38 wild ancestors captured between 1982 and 85 near Linville NC. Third to fifth generations in captivity.
<i>P. maniculatus</i> X <i>P. polionotus</i> F <sub>1</sub> Hybrids	Sometimes available.

MUTATIONS IN THE SOUTH CAROLINA STOCK CENTER:

<u>Coat Colors</u>	<u>ORIGINAL SOURCE</u>
Albino c/c	Sumner's albino deer mice (Sumner, 1922)
Black (Non-agouti) a/a	Horner's black mutant (Horner et al., 1980)
Blonde bl/bl	Mich. State colony (Pratt and Robbins, 1982)
Brown b/b	Huestis stocks (Huestis and Barto, 1934)
Dominant spotting S/-	Wild caught in Illinois (Feldman, 1936)
Gray g/g	Natural polymorphism. From Dice stocks (Dice, 1933)
Ivory i/i	Wild caught in Oregon. (Huestis, 1938)
Pink-eyed dilution p/p	Sumner's "pallid" deer mice. (Sumner, 1917)
Platinum pt/pt	Barto stock at U. Mich. (Dodson et al., 1987)
Silver si/si	Huestis stock. (Huestis and Barto, 1934)
White-belly non-agouti a <sup>w</sup> /a <sup>w</sup>	Egoscue's "non-agouti" (Egoscue, 1971)
Wide-band agouti A <sup>wb</sup> /-	Natural polymorphism. Univ. Michigan stock (McIntosh, 1954)
Yellow y/y	Sumner's original mutant. (Sumner, 1917)

Note: Some of the coat color 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 Mutants and Variants

ORIGIN

Alcohol dehydrogenase negative  
Adh<sup>o</sup>/Adh<sup>o</sup>

South Carolina BW stock.  
(Felder, 1975)

Alcohol dehydrogenase positive  
Adh<sup>r</sup>/Adh<sup>r</sup>

South Carolina BW stock.  
(Felder, 1975)

Epilepsy ep/ep

U. Michigan artemisiae stock.  
(Dice, 1935)

Flexed-tail\* f/f

Probably derived from Huestis  
flexed-tail (Huestis and  
Barto, 1936)

Hairless-2 hre/hre\*\*

Egoscue's hairless  
(Egoscue, 1962)

Juvenile ataxia ja/ja

U. Michigan stock.  
(VanOoteghem, 1983)

Enzyme variants. Wild type stocks given above provide a reservoir for several enzyme and other protein variants. See Dawson, et al. (1983).

\*Available only on pink-eye dilution background.

\*\*Temporarily unavailable.

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Limited numbers of other stocks, species, mutants 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:

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William Franklin Blair

PEROMYSCUS  
PIONEER

W. Frank Blair

1912 - 1985

In the front ranks of researchers who left a lasting imprint upon Peromyscus biology is William Franklin Blair. Blair's prolific field and laboratory investigations conducted during the early years of his career were the first to fully integrate ecology, genetics and behavior of deer mice and their allies into an evolutionary framework. His 1950 landmark paper "Ecological Factors in Speciation of Peromyscus" (*Evolution*, 4:253-275) stimulated much subsequent research and strongly influenced the next generation of peromyscologists. Nor was this his only contribution to our knowledge of Peromyscus. Blair published numerous papers on Peromyscus, including his classic investigations of beach mice on Santa Rosa Island FL (1951. *Contr. Lab. Vert. Biol.*, 48:1-47) and deer mice in Tularosa Basin NM (1943, 1947. *Contr. Lab. Vert. Biol.*, 21:1-40; 35:1-17; 36:1-16). He was among the first to recognize the role of behavior in species isolation and, with his mentor Lee R. Dice, helped establish Peromyscus as a model for mammalian speciation research.

Frank Blair, the oldest of five children, was born 25 June 1912 at Dayton, Texas, but moved with his family in 1916 to a 10-acre strawberry farm near Westville, Oklahoma. It was here he spent his early boyhood and in this rural setting developed a lasting fascination with nature. At age ten the family again moved, this time to Tulsa. Here he attended high school and completed his undergraduate degree at the University of Tulsa. His interest in biology was further whetted by a course in zoology taught by H.D. Chase and another in botany with B.D. Barclay. While an undergraduate he met Fern Antel, who was a university librarian, and they were soon married. In 1934 Blair entered graduate school at the University of Florida at Gainesville and received a master's degree in 1936. His thesis work on ecology of the marsh rabbit in Florida was conducted under the supervision of H.B. Sherman, inventor of the Sherman live trap and a protege of Lee Dice. About this time Blair published his first Peromyscus paper, a brief note co-authored with John Kilby, "The gopher mouse - Peromyscus floridanus" (1936. *J. Mamm.*, 17:421-422).

Blair then enrolled as a doctoral student at the University of Michigan to work under the direction of Dice. Thus began a productive association which generated numerous studies of Peromyscus and other small mammals. Blair received the Ph.D. in 1938, writing his dissertation on ecological relationships of mammals in northeastern Oklahoma, but remained at Ann Arbor as a Research Associate until the summer of 1942 when he entered the Army Air Corps during World War II. It was during this pre-war interval that Blair conducted most of his Peromyscus work, although much of it was not published until after his release from active duty.

Blair's major contribution to Peromyscus biology was his ability to combine incisive field observations with laboratory behavior and breeding studies and from these develop an understanding about evolution of a species as an entirety. His actual Peromyscus research centered on the three subspecies he studied most intensely: P. maniculatus bairdii in southern Michigan; P. m. blandus in Tularosa Basin New Mexico; and P. polionotus leucocephalus on Santa Rosa Island, Florida. However, Blair, interacting with Dice and others in the Michigan group at that time, had a broader perspective of evolution in the genus than his immediate research projects might suggest. In his field studies he employed trap-mark-release-repeated recapture methods tracking individuals. His wife often accompanied him and acted as his field assistant. Blair generally returned live animals to the laboratory where genetic and behavioral studies were accomplished. His published accounts of his field observations make for fascinating reading and convey a sense of intimacy with the animals as individuals.

From 1938 through 1942 Blair was involved more or less continuously with small mammal ecology in field and woodland habitats in Michigan near Ann Arbor. Several published papers resulted including "A Study of Prairie Deer-Mouse Populations in Southern Michigan" (1940. *Am. Mid. Nat.*, 24:273-305), his first detailed investigation of a Peromyscus population. During this period Blair also made extended expeditions of two and three months duration to the Tularosa Basin in 1938 and 1940. He calculated home ranges, estimated population numbers and densities and recorded breeding and age structure. He confirmed that buff and gray coat color polymorphism in P. m. blandus was correlated with soil color, and estimated the allelic frequencies of the genes involved. This was among the first gene frequency studies in mammalian populations. He also documented the case of a single young female which moved nearly a half mile between study plots on each of four occasions within a three week interval, perhaps a record for deer mice. Blair's Peromyscus field studies culminated with two trips (5 Nov 1941 - 13 Jan 1942; 7 May - 17 June 1942) to the gulf shores of Florida where he analyzed the structure of beach mouse (P. polionotus leucocephalus) populations on Santa Rosa Island. Among many other observations he noted that permanent bonding was usual between pairs of these mice, now recognized as typical in P. polionotus generally. Upon returning to Ann Arbor, he initiated an experiment on behavioral isolation between P. polionotus leucocephalus and P. maniculatus blandus in special test cages. Blair entered the military at this time and the study was concluded by Walter E. Howard (1944. *Contrib. Lab. Vert. Biol.*, 26:1-19). This behavioral isolation study portended the direction of Blair's well-known later work with anurans.

In addition to the population studies, Blair described the formal genetics of the white cheek gene identified in the beach mouse, and the brown-tip trait in the deer mouse. The latter proved to be a recurrence of the brown mutant originally described by Huestis and Barto (1934). He was the first (1942. *J. Mamm.*, 23:196-204) to convincingly argue, based on structure of the baculum, that the golden mouse (Ochrotomys nuttalli) was not a Peromyscus, a conclusion now generally accepted. He described P. comanche as a species separate from P. truei (1943. *Contrib. Lab. Vert. Biol.*, 24:1-8), a distinction later debated. Most significantly by the early 1940's he was developing major insights into speciation and the nature of species and races.

His first review paper in this direction, "Criteria for Species and their Subdivisions from the Point of View of Genetics" (1943. *Annals N.Y. Acad. Sci.*, 44:179-188) revived the "cenospecies" concept. Cenospecies are groups of species which are at least partially interfertile. In Peromyscus the cenospecies corresponds approximately to the species group. In this paper Blair adopted the mainstream neodarwinian philosophy flourishing among his contemporaries. By the late 1940's he had formulated a comprehensive view of Peromyscus speciation as reflected in the classic 1950 Evolution paper cited earlier and in several other papers published during the 1950s. One of his major themes stressed the strong association of present-day distributions and recent speciation events in North America with late Pleistocene climate and vegetation. Overall, Blair published 22 papers devoted primarily to Peromyscus and another dozen involved or related to the genus in significant fashion.

After service as a survival training officer during the war, Blair returned for a few months to his position at the Laboratory of Vertebrate Biology at Michigan, but then joined the faculty at the University of Texas in autumn 1946. Although Blair continued to conduct some studies with mammals and published a number of significant papers based on his earlier studies, his research focus shifted to anurans and the role of mating calls in species recognition. Undoubtedly he was influenced in this course by his younger brother, A. P. Blair, who was already a recognized authority amphibian biology. Frank Blair's work with the genus Bufo became particularly well known and he authored numerous articles on amphibians. In the latter part of his active career he became increasingly involved with the International Biological Program and other conservation efforts. He frequently testified before legislative bodies or other groups in behalf of environmental concerns. Blair was also highly regarded as a teacher. Although somewhat of a loner and occasionally aloof, he could also be an affable individual who made student and colleague alike feel at ease. He supervised the graduate studies of 100 students, about half of which were Ph.D. candidates. Among his graduate students who worked with Peromyscus were W.H. McCarley, W.K. Clark, J.R. Tamsitt, W.N. Bradshaw and R.E. Moore. Blair's lifetime publication list totaled about 160 titles, very few of which were co-authored. He was one of five authors of a widely used reference book, Vertebrates of the United States.

Frank Blair was highly esteemed among zoologists, ecologists and evolutionists. He received numerous honors and recognitions, including the 1975 AIBS Distinguished Service Award and the 1977 Joseph Priestly Award. He served as president of the American Institute of Biological Sciences (1972), the Ecological Society of America (1963), the Society for the Study of Evolution (1962) and the Southwestern Association of Naturalists (1953-55). He also served in various offices and on numerous committees of national and local organizations.

After a productive 36-year career on the University of Texas faculty Frank Blair retired, shortly before the death of his wife, in 1982. His health declined rapidly after this time and he passed away February 9, 1985. He had no children and left his 10-acre homestead, which he had carefully nurtured as a preserve, to the local Audubon Society. W. Frank Blair also left an immense legacy in the students he trained and in the clear insights he provided into the social and genetic organization of vertebrate populations.



## GENETIC LOCI IN THE DEER MOUSE

(*Peromyscus maniculatus*)

Tables Ia through Id list genetic loci described in *Peromyscus maniculatus* and other species of the *maniculatus*-group. This list is limited to loci formally recognized from genetic crosses accomplished in the laboratory and reported in the published scientific literature. Additional genetic traits are known and some have been cited in abstracts, casual reports, newsletters, grant proposals, papers presented at meetings, etc. The latter are not included here since the pertinent information is incomplete.

Table II lists presumptive variant protein loci described in natural populations of *P. maniculatus* and other members of the *maniculatus*-species group. These loci may or may not have been formally analyzed by mendelian crosses. Monomorphic (invariant) protein loci are not listed. Only published reports are included.

Although the genetic nomenclature of *Peromyscus* is not yet completely standardized, the conventions used for the house mouse (*Mus*) are employed wherever possible. In designating genetic loci we adopted the symbols given by the original investigator, unless there is clear homology with *Mus* or the original symbols have been superseded by subsequent usage. In the latter case we have adopted the most recently used. If a variant is shown to be allelic with a previously reported gene, the locus symbol is reduced to an allelic symbol. Where two authors have used the identical symbol for different loci we have given priority to the first reported, and devised an alternate designation for the other.

References cited in the tables are available in **BIBLIOGRAPHY OF PEROMYSCUS (RODENTIA): GENETICS** compiled by Bruce Buttler, Biology Department, Canadian Union College, College Heights, Alberta, Canada, TOC OZO.

TABLE 1A  
Coat color and pattern, and eye pigmentation variants

Name of locus and alleles	Symbol	Mode of inheritance	Linkage group	Original description and analysis	Collateral descriptions, interactions, and recurrences	Recombination reported
AGOUTI			III			
Wide-band agouti	A <sup>Nb</sup>	dominant		McIntosh (1956a)	Blair (1947) as "buff"	Clark (1938) as "buff"; Barto (1956)
White belly non-agouti	a <sup>w</sup>	recessive		Egoscue (1971)		
Non-agouti (Black)	a	recessive		Horner <i>et al.</i> (1980)		
BROWN			II			
	b	recessive		Huestis and Barto (1934)	Blair (1947); McIntosh (1956a); Dawson <i>et al.</i> (1969)	Huestis and Barto (1934); Blair (1947); Barto (1955, 1956); McIntosh (1956a)
Orange-tan	b <sup>ot</sup>	recessive		Egoscue and Day (1958)		
BLOND				Pratt and Robbins (1982)		
ALBINO			I			
	c	recessive		Sumner (1922)		Sumner (1922); Clark (1936, 1938); Feldman (1937); Barto (1942a); Huestis and Lindstedt (1946); Huestis (1946)
COLORLESS HAIR TIP*	ctp	recessive		Bowen and Dawson (1969)	Bowen (1968)	
DILUTE*			II			
	d	recessive		Dice (1933)		Clark (1938); Barto (1942a, 1956); McIntosh (1956a)
GRAY						
	g	recessive		Dice (1933)	Clark (1938); Blair (1947); McIntosh (1956a)	Blair (1944, 1947)
IVORY						
	i	recessive		Huestis (1938)	Clark (1938)	Barto (1942a; 1956); McIntosh (1956a)
PINK-EYED DILUTION			I			
	p	recessive		Sumner (1917)	Barto (1942b)	Sumner (1922); Clark (1936, 1938); Feldman (1937); Snyder (1980a)
PLATINUM						
	pt	recessive		Dodson <i>et al.</i> (1987)		
RED EYE (Heterochromia)						
	r	recessive		Huestis and Willoughby (1950)		
DOMINANT SPOT (Whiteface)						
	s	dominant		Feldman (1936)	Haddock (1966)	Feldman (1937)
SILVER			I			
	si	recessive		Huestis and Barto (1934)		Huestis and Barto (1934); Huestis and Piestrak (1942); Huestis and Lindstedt (1946); Barto (1956)
WHITE CREEK						
	wc	dominant		Blair (1944)	Bowen and Dawson (1977)	Blair (1944)
WHITESIDE*						
	wh	recessive		McIntosh (1956b)		
YELLOW						
	y	recessive		Sumner (1917)	Sumner and Collins (1922); McIntosh (1956a)	Sumner (1922); Feldman (1937); (1956a); Barto (1956)
COMPLEXLY INHERITED TRAITS:						
Minor white spotting (star, splash, etc.)	p-1; p-2	recessive incompletely penetrant		Feldman (1936)	Sumner (1932); Barto and Huestis (1933)	
Grizzled*	"g"	"complex dominant"		Sumner (1932)		
Coat pattern in <i>P. polionotus</i>						
Pointed A	Pa	dominant	VII	Bowen and Dawson (1977)	Bowen (1968)	Bowen and Dawson (1977)
Pointed B	Pb	dominant	VII			
Tapered	Pp	dominant				
Coat pattern modifiers in <i>P. polionotus</i>						
Squared modifier	Rs	incompletely dominant		Bowen and Dawson (1977)		
Tapered modifier	Rt	dominant				

\*No longer known to be in existence.

TABLE 1B  
Integumentary, skeletal and metabolic variants

Name of locus and alleles	Symbol	Mode of inheritance	Linkage group	Original description and analysis	Collateral descriptions, interactions, and recurrences	Recombination reported
CATARACT-WEBBED (syndactyly)	<i>cw</i>	recessive		Anderson and Burns (1979)		
FLEXED-TAIL	<i>f</i>	recessive	I	Huestis and Barto (1936a)		Huestis and Barto (1936a); Huestis and Piestrak (1942); Huestis and Lindstedt (1946); Huestis (1946); Huestis, <i>et al.</i> (1956); Barto (1956)
HAIRLESS-1	<i>hr-1</i>	recessive		Sumner (1924)		Sumner 1924, 1932; Feldman (1937); Clark (1938); Barto (1942a, 1955, 1956); McIntosh (1956a)
HAIRLESS-2	<i>hr-2</i>	recessive		Egoscue (1962)		
NUDE* (post-juvenile)	<i>n</i>	recessive		Clark (1938)	Barto (1942a)	
SPHEROCYTOSIS (Hereditary jaundice)	<i>sph</i>	recessive		Huestis and Anderson (1954)	Huestis, <i>et al.</i> (1956); Motulsky, <i>et al.</i> (1956)	Huestis, <i>et al.</i> (1956)

TABLE 1C  
Behavioral and Neurological Variants

Name of locus and alleles	Symbol	Mode of inheritance	Linkage group	Original description and analysis	Collateral descriptions, interactions, and recurrences	Recombination reported
BOGGLER	<i>bg</i>	recessive		Barto (1955)	Vandermerer and Barto (1969)	Barto (1955)
EPILEPSY (EP)	<i>ep</i> , ( <i>e</i> , <i>v</i> <sub>2</sub> )	recessive		Dice (135)	Clark (1938); Watson (1939); Chance & Yaxley (1950); Barto (1954, 1956)	Watson (1939); Barto (1956)
JUVENILE ATAXIA	<i>ja</i>	recessive		Van Ooteghem (1983)		
SPINNER*	<i>sp</i> ( <i>v</i> <sub>3</sub> )	recessive		Watson (1939)	Barto (1954)	
TREMOR*	<i>t</i>	recessive		Huestis and Barto (1936b)		
WALTZER* (waltzing in <i>bairdii</i> )	<i>v</i> ( <i>w</i> )	recessive	III	Dice (1935)	Clark (1938); Watson (1939); Barto (1942a, 1954, 1956); McIntosh (1956)	

\*No longer known to be in existence.

Table 1D

Biochemical and immunological genetic variants formally analyzed in the *Peromyscus maniculatus* species group

Name of Locus	Allelic designation	Linkage group	Description and formal analysis	Recombination Reported
ALCOHOL DEHYDROGENASE (liver)	$Adh-1^f$ $Adh-1^s$ $Adh-1^o$	VI	Felder (1975); Burnett and Felder (1978a; 1978b)	Dawson <i>et al.</i> (1983)
ALBUMIN (serum)	$Alb^{100}$ $Alb^{96}$ $Alb^{86}$	VI	Brown and Welser (1968); Jensen and Rasmussen (1971)	Dawson (1982); Dawson <i>et al.</i> (1983)
AMYLASE (salivary)	$Amy-1^a$ $Amy-1^b$ $Amy-1^c$	VI	Evans <i>et al.</i> (1977)	Dawson <i>et al.</i> (1983)
ESTERASE (erythrocytic)	$Es-1^o$ $Es-1^a$ $Es-1^b$	IV	Randerson (1965); Van Deussen and Kaufmann (1978)	Randerson (1973)
ESTERASES (tissue and serum)	Es-2 through Es-7 (Symbols not standardized)		Rasmussen and Jensen (1971); Dawson (1982); Gill (1976); Baccus <i>et al.</i> (1980)	Dawson (1982)
GLUTAMATE OXALOACETATE TRANSAMINASE (soluble)	$Got-1^a$ $Got-1^b$ $Got-1^c$		Gill (1976)	Dawson <i>et al.</i> (1983)
AUTOSOMAL GLUCOSE-6-PHOSPHATE DEHYDROGENASE (soluble)	$G6pd-1^a$ $G6pd-1^b$		Shaw and Barto (1965); Shaw (1966)	
$\alpha$ -GLYCEROPHOSPHATE DEHYDROGENASE (tissue)	$Gpd-1^a$ $Gpd-1^b$		Gill (1976)	
HEMOGLOBIN - ALPHA TYPE GLOBINS (Duplicated locus)	$Hba^1 = (Hb^r) = (Hb, I^a)$ $Hba^2$ $Hbc^0 = (Hb^0) = (Hb, I^0)$ $Hbc^1$ $Hbc^2 = (Hb^f)$		Thompson <i>et al.</i> (1966) Rasmussen <i>et al.</i> (1968) Jensen <i>et al.</i> (1976) Maybank and Dawson (1976) Snyder (1978; 1980b)	
HEMOGLOBIN - BETA TYPE GLOBINS (Tripllicated locus)	$Hbb^1$ $Hbd^0$ $Hbd^1$ or $Hbb-b1$ $Hbe^0$ or $Hbb-b2$ $Hbe^1$ or $Hbb-b3$	I	Snyder (1978; 1980b) Fadgett <i>et al.</i> (1987)	Snyder (1980a)
HAPTOGLOBIN (serum)	$Hpt^1$ $Hpt^2$		Rasmussen (1968); Griswold and Dawson (1971)	
IMMUNOGLOBIN (7S <sub>Y1</sub> )	$Ig^f$ $Ig^s$		Coe (1972)	
LACTATE DEHYDROGENASE A SUBUNIT (tissue)	$Ldh-A^a$ $Ldh-A^b$		Cattanach and Perz (1969)	
LACTATE DEHYDROGENASE B SUBUNIT (tissue)	$Ldh-B^f$ $Ldh-B^s$		Shaw and Barto (1963)	
LEUCINE AMINO PEPTIDASE (serum)	$Lap-1^a$ $Lap-1^b$	V	Dawson (1982)	Dawson (1982); Dawson <i>et al.</i> (1983)
SUPEROXIDE DISMUTASE	$Sod-1^J = (Ng^J)$ $Sod-1^P = (Ng^P)$ $Sod-1^M = (Ng^M)$		Birdsall <i>et al.</i> (1970)	
6-PHOSPHOGLUCONATE DEHYDROGENASE (tissue)	$6-Pgd^a$ $6-Pgd^b$		Gill (1976)	Dawson <i>et al.</i> (1983)
PHOSPHOGLUCOMUTASE-1 (tissue)	$Pgm-1^a$ $Pgm-1^b$		Gill (1976)	
PHOSPHOGLUCOMUTASE-4 (tissue)	$Pgm-4^a$ $Pgm-4^b$ $Pgm-4^c$		Gill (1976)	
ERYTHROCYTTIC ANTIGEN	$Pm^A$ $Pm^B$ $Pm^C$ $Pm$	IV	Rasmussen (1961) Savage and Cameron (1971)	Randerson (1973)
TRANSFERRIN (serum)	$Trf^a = (Trc^J)$ $Trf^b$ $Trf^c$ $Trf^e$ $Trf^m$ $Trf^f$	V	Rasmussen and Koehn (1966) Biggers and Dawson (1971) Griswold and Dawson (1971) Canham <i>et al.</i> (1970)	Dawson (1982); Dawson <i>et al.</i> (1983)

Table II GENETICALLY VARIANT ENZYME AND OTHER PROTEIN LOCI REPORTED  
IN NATURAL POPULATIONS OF PEROMYSCUS MANICULATUS AND  
OTHER MEMBERS OF THE MANICULATUS-SPECIES GROUP.

Protein	Locus Symbol	Species	References
ALBUMIN	Aib-1	<i>P. maniculatus</i> <i>P. polionotus</i>	Rasmussen (1970) Jensen and Rasmussen (1971) Selander et al. (1971) Biggers and Dawson (1971) Loudenslager (1978) Baccus et al. (1980)
ALCOHOL DEHYDROGENASE	Adh-1	<i>P. maniculatus</i> <i>P. melanotis</i>	Avise et al. (1979) Baccus et al. (1980)
AMYLASE	Amy-1	<i>P. maniculatus</i>	Aquadro and Patton (1980)
ESTERASE	Es-1 Es-2 Es-3 Es-4 Es-5 Es-6 Es-7 Es-8	<i>P. maniculatus</i> <i>P. polionotus</i>	Rasmussen and Jensen (1971) Selander et al. (1971) Peck and Biggers (1975) Gill (1978) Loudenslager (1978) Foltz (1981)
GLUTAMATE OXALOACETATE TRANSAMINASE	Got-1	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Selander et al. (1971) Gill (1978) Loudenslager (1978) Avise et al. (1979) Baccus et al. (1980)
GLUCOSE 6-PHOSPHATE DEHYDROGENASE	G6pd-1 (H6pd-1)	<i>P. maniculatus</i>	Shaw and Barfo (1985) Loudenslager (1978)
GLUCOSE PHOSPHATE ISOMERASE	Gpi-1 (Pgi-1)	<i>P. polionotus</i> <i>P. melanotis</i>	Selander et al. (1971) Avise et al. (1979) Foltz (1981)
α-GLYCEROPHOSPHATE DEHYDROGENASE	Gpd-1	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. oreas</i>	Selander et al. (1971) Mascarello and Shaw (1973) Gill (1978) Avise et al. (1979)
HAPTOGLOBIN	Hpt	<i>P. polionotus</i>	Peck and Biggers (1975)
HEMOGLOBIN	Hba Hbb	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Thompson et al. (1966) Ahl (1968) Foreman (1968) Rasmussen et al. (1968) Rasmussen (1970) Selander et al. (1971) Snyder (1977, 1980) Loudenslager (1978) Avise et al. (1979) Chappell and Snyder (1984)
ISOCITRATE DEHYDROGENASE	Idh-1	<i>P. maniculatus</i> <i>P. oreas</i> <i>P. polionotus</i> <i>P. sejugis</i>	Mascarello and Shaw (1973) Baccus et al. (1980) Avise et al. (1974)
LACTATE DEHYDROGENASE	Ldh-1 Ldh-2	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Selander et al. (1971) Avise et al. (1979)
MALATE DEHYDROGENASE	Mdh-1 Mdh-2	<i>P. polionotus</i>	Selander et al. (1971)
PEPTIDASE	Pep-1 (Pep-B)	<i>P. maniculatus</i> <i>P. melanotis</i>	Avise et al. (1979) Baccus et al. (1980)
6-PHOSPHOGLUCONATE DEHYDROGENASE	Pgd-1	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. oreas</i>	Selander et al. (1971) Mascarello and Shaw (1973) Gill (1978) Avise et al. (1979) Baccus et al. (1980) Foltz (1981)
PHOSPHOGLUCOMUTASE	Pgm-1 Pgm-2 Pgm-3 Pgm-4	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Selander et al. (1971) Mascarello and Shaw (1973) Gill (1978) Avise et al. (1979)
SORBITOL DEHYDROGENASE	Sdh-1	<i>P. maniculatus</i>	Baccus et al. (1980)
TRANSFERRIN	Trf	<i>P. maniculatus</i> <i>P. polionotus</i>	Rasmussen (1970) Biggers and Dawson (1971) Selander et al. (1971) Gill (1978) Redfield (1976) Loudenslager (1978) Avise et al. (1979) Baccus et al. (1980) Foltz (1981)
Miscellaneous Non-specific Proteins		<i>P. maniculatus</i>	Mascarello and Shaw (1973) Gill (1978)

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## EXPERIMENTAL SPECIES HYBRIDIZATION IN PEROMYSCUS

The following pages summarize published reports of interspecific hybridization experiments involving Peromyscus. Some of the hybridization attempts were conducted in connection with research done for other purposes, for example gene mapping or embryological studies. In addition to the interspecific crosses given here, there are many reports of hybridization between subspecies which we have not addressed in this issue of PEROMYSCUS NEWSLETTER. We expect to survey these in a future issue.

The references cited in the tables are listed in "Bibliography of Peromyscus (Rodentia): Genetics" by Bruce Buttler of Canadian Union College. We are aware of several unpublished interspecific hybrid experiments with Peromyscus, but have omitted these from the listing in the tables.

Most reported attempts of Peromyscus species hybridization have not produced liveborn offspring. Some attempts have involved early embryonic development or in vitro fertilization, from which no attempt was made to secure mature hybrid animals. Viable - i.e. weaned, but not necessarily fertile - progeny have been obtained from the following Peromyscus species crosses:

P. eremicus X P. interparietalis

P. guardia X P. interparietalis

P. guardia X P. collatus

P. truei X P. difficilis

P. leucopus X P. gossypinus

P. maniculatus X P. polionotus

P. maniculatus X P. melanotis

P. maniculatus X P. oreas

See tables for more details and literature citations.

SUMMARY OF EXPERIMENTAL INTERSPECIFIC HYBRIDIZATION ATTEMPTS IN PEROMYSCUS

CROSS (FEMALE X MALE)	COMMENTS	REFERENCES
INTERGENERIC AND INTERSUBGENERIC CROSSES.		
<u>P. maniculatus</u> X <u>Mus (musculus) domesticus</u>	Artificial insemination. Five mice. No results.	Maddock & Dawson (1974)
<u>Mus (musculus) domesticus</u> X <u>P. maniculatus</u>	In vitro fertilization. 100 ova. No results.	Fukuda et al. (1979)
<u>Mus (musculus) domesticus</u> X <u>P. maniculatus</u>	In vitro fertilization. 167 ova. No results.	Hanada and Chang (1978)
<u>Mus (musculus) domesticus</u> X <u>P. polionotus</u>	In vitro fertilization. 261 ova. No results.	Fukuda et al. (1979)
<u>Mus (musculus) domesticus</u> X <u>P. leucopus</u>	In vitro fertilization. 167 ova. No results.	Hanada and Chang (1978)
<u>P. maniculatus</u> X <u>Rattus norvegicus</u>	Artificial insemination. Five mice. No results.	Maddock and Dawson (1974)
<u>Rattus norvegicus</u> X <u>P. maniculatus</u>	In vitro fertilization. 108 ova. No results.	Hanada and Chang (1978)
<u>Rattus norvegicus</u> X <u>P. maniculatus</u>	In vitro sperm injection. 17/67 ova normal pronuclei.	Thadana (1980)
<u>Rattus norvegicus</u> X <u>P. leucopus</u>	In vitro fertilization. Sperm penetration. 18/164 ova.	Hanada and Chang (1978)
<u>P. maniculatus</u> X <u>Meriones unguiculatus</u>	Artificial insemination. Six mice. No results.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>Mesocricetus auratus</u>	Artificial insemination. First cleavage. 2/18 mice.	Maddock and Dawson (1974)
<u>Mesocricetus auratus</u> X <u>P. maniculatus</u>	In vitro fertilization. Sperm penetration. 271/867 ova.	Hanada and Chang (1978)
<u>Mesocricetus auratus</u> X <u>P. leucopus</u>	In vitro fertilization. Sperm penetration. 2/200 ova.	Hanada and Chang (1978)
<u>P. maniculatus</u> X <u>Oryzomys palustris</u>	Artificial insemination. First cleavage. 2/6 mice.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>Sigmodon hispidus</u>	Artificial insemination. First cleavage. 1/12 mice.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>Ochrotomys nuttalli</u>	Artificial insemination. Seven mice. No results.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>Reithrodontomys humilis</u>	Artificial insemination. Sperm penetration. 1/6 mice.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>P. (Podomys) floridanus</u>	Artificial insemination. 2nd - 3rd cleavage. 1/6 mice.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>P. (Haplomyloms) eremicus</u>	Caged pairs. No progeny. 29 attempts.	Dice (1933)
<u>P. leucopus</u> X <u>P. (Haplomyloms) eremicus</u>	Caged pairs. No progeny. 24 attempts.	Dice (1933)

INTERSPECIFIC CROSSES WITHIN SUBGENUS HAPLOMYLOMYS.

(FEMALE X MALE)

	COMMENT	REFERENCE
<u>P. eremicus</u> X <u>P. californicus</u>	Six caged pairs. No progeny.	Dice (1933)
<u>P. eremicus</u> X <u>P. interparietalis</u>	Five caged pairs. Nine progeny. F <sub>1</sub> fertile.	Brand and Ryckman (1969)
<u>P. eremicus</u> X <u>P. interparietalis</u>	Two caged pairs. No progeny.	Lawlor (1971)
<u>P. interparietalis</u> X <u>P. eremicus</u>	Five caged pairs. 17 progeny. F <sub>1</sub> fertile.	Brand and Ryckman (1969)
<u>P. interparietalis</u> X <u>P. eremicus</u>	Two caged pairs. No progeny.	Lawlor (1971)
<u>P. eremicus</u> X <u>P. guardia</u>	Five caged pairs. No progeny.	Brand and Ryckman (1969)
<u>P. guardia</u> X <u>P. eremicus</u>	Five caged pairs. No progeny.	Brand and Ryckman (1969)
<u>P. eremicus</u> X <u>P. collatus</u>	Four caged pairs. No progeny.	Lawlor (1971)
<u>P. collatus</u> X <u>P. eremicus</u>	Three caged pairs. No progeny.	Lawlor (1971)
<u>P. interparietalis</u> X <u>P. guardia</u>	Five caged pairs. No progeny.	Brand and Ryckman (1969)
<u>P. guardia</u> X <u>P. interparietalis</u>	Five caged pairs. No progeny. One mass mating. Two litters.	Brand and Ryckman (1969)
<u>P. guardia</u> X <u>P. interparietalis</u>	Caged pair. No progeny.	Lawlor (1971)
<u>P. interparietalis</u> X <u>P. collatus</u>	Caged pair. Progeny viable.	Lawlor (1971)
<u>P. collatus</u> X <u>P. interparietalis</u>	Caged pair. No progeny.	Lawlor (1971)

INTERSPECIES-GROUP CROSSES.

(FEMALE X MALE)

	COMMENT	REFERENCES
<u>P. boylii</u> X <u>P. (comanche) truei</u>	Caged pairs. No progeny. 9 attempts.	Blair (1943)
<u>P. maniculatus</u> X <u>P. truei</u>	Artificial insemination. Early cleavage 9/30 attempts.	Maddock and Dawson (1974)
<u>P. leucopus</u> X <u>P. maniculatus</u>	Caged pairs. No progeny. 69 attempts.	Dice (1933)
<u>P. maniculatus</u> X <u>P. leucopus</u>	Artificial insemination. 44 attempts. 1 to term, not viable. 13 to mid-gestation.	Dawson et al. (1972), Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>P. gossypinus</u>	Artificial insemination. 24 attempts. 13 early cleavage. 1 implantation.	Maddock and Dawson (1974)

INTERSPECIFIC CROSS ATTEMPTS WITHIN THE P. TRUEI SPECIES GROUP.

(FEMALE X MALE)	COMMENT	REFERENCE
<u>P. truei</u> X <u>P. (nasutus) difficilis</u>	Caged pairs. 3/17 fertile. F <sub>1</sub> females fertile, males sterile.	Dice and Liebe (1937)
<u>P. truei</u> X <u>P. (nasutus) difficilis</u>	Two pairs in social choice cages. No hybrids detected/67 progeny.	Tamsitt (1961)
<u>P. truei</u> X <u>P. (nasutus) difficilis</u>	F <sub>1</sub> females fertile, males sterile, with impaired spermatogenesis. 90% reduction in F <sub>1</sub> progeny.	Moree (1946, 1948)

INTERSPECIFIC CROSS ATTEMPTS WITHIN THE P. BOYLLI SPECIES GROUP.

(FEMALE X MALE)	COMMENT	REFERENCE
<u>P. boyllii</u> X <u>P. stephani</u>	Two caged pairs. No progeny.	Lawlor (1971)
<u>P. stephani</u> X <u>P. boyllii</u>	One caged pair. No progeny.	Lawlor (1971)

INTERSPECIFIC CROSS ATTEMPTS WITHIN THE P. LEUCOPUS SPECIES GROUP.

(FEMALE X MALE)	COMMENT	REFERENCE
<u>P. leucopus</u> X <u>P. gossypinus</u>	70 F <sub>1</sub> hybrids produced. F <sub>2</sub> produced.	Dice (1937)
<u>P. leucopus</u> X <u>P. gossypinus</u>	Three F <sub>1</sub> hybrids produced.	Foreman (1966)
<u>P. leucopus</u> X <u>P. gossypinus</u>	Thirty-nine mating choice cages. No hybrids detected among 25 progeny.	Bradshaw (1968)

INTERSPECIFIC CROSS ATTEMPTS WITHIN THE P. MANICULATUS SPECIES GROUP.

(FEMALE X MALE)	COMMENT	REFERENCE
<u>P. maniculatus</u> X <u>P. polionotus</u>	Viable, fertile F <sub>1</sub> from 1 of "a number" of caged pairs.	Summer (1930, 1932)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Progeny from one of five caged pairs.	Dice (1933)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Progeny from seven of 23 caged pairs. F <sub>1</sub> fertile.	Watson (1942)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Viable progeny from 20 of an unknown number. Some F <sub>1</sub> males sterile.	Blair and Howard (1944), Blair (1944)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Viable progeny from 10 of 31 caged pairs.	Liu (1953a)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Viable progeny from 20 of 44 caged pairs. Some F <sub>1</sub> pre-weaning mortality. F <sub>1</sub> average smaller than either species. Successful backcrosses to either species and F <sub>2</sub> produced.	Dawson (1965, 1966, 1971)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Viable, fertile progeny from 1 of 20 caged pairs homozygous for the brown mutation.	Dawson et al. (1969)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Viable F <sub>1</sub> progeny from 17 of 30 caged pairs. Near-term fetuses and placentas collected from six matings. F <sub>1</sub> fetal and placental weights less than in either species. Placenta compact.	Rogers and Dawson (1970)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Karyotype of F <sub>1</sub> female given.	Te and Dawson (1971)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Nine F <sub>1</sub> hybrids produced in test of transferrin inheritance.	Griswold and Dawson (1971)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Artificial insemination. 10 of 12 fertile.	Maddock and Dawson (1974)
<u>P. maniculatus</u> X <u>P. polionotus</u>	41 F <sub>1</sub> hybrids produced in test of alcohol dehydrogenase inheritance.	Felder (1975), Burnett and Felder (1978)
<u>P. maniculatus</u> X <u>P. polionotus</u>	In vitro fertilization. 89 of 115 ova fertilized, 79 normal, 8 abnormal.	Fukuda et al. (1979)
<u>P. maniculatus</u> X <u>P. polionotus</u>	Seven of 24 caged pairs pregnant. 37 of 38 embryos survived to term.	Maddock and Chang (1979)
<u>P. maniculatus</u> X <u>P. polionotus</u>	87 F <sub>1</sub> neonates and 47 fetuses measured in test of transspecific immunity.	Dawson et al. (1982)
<u>P. maniculatus</u> X <u>P. polionotus</u>	F <sub>1</sub> hybrids and backcrosses to <u>P. maniculatus</u> produced in genetic linkage tests.	Dawson (1982), Dawson et al. (1983)
<u>P. maniculatus</u> X <u>P. polionotus</u>	15 pregnant females assayed for progesterone.	Bell and Dawson (1983)



INTERSPECIFIC CROSSES WITHIN THE P. MANICULATUS SPECIES GROUP (Continued):

(FEMALE X MALE)	COMMENT	REFERENCE
<u>P. maniculatus</u> X <u>P. melanotus</u>	Viable progeny from one of two caged pairs. Male F <sub>1</sub> fertile in backcross to <u>P. maniculatus</u> .	Clark (1966)
<u>P. maniculatus</u> <sup>1</sup> X <u>P. melanotus</u>	No progeny from 137 pairs.	Bowers et al. (1973), Bowers (1974)
<u>P. maniculatus</u> <sup>1</sup> X <u>P. oreas</u>	No progeny from 12 pairs.	Dice (1949)
<u>P. maniculatus</u> X <u>P. oreas</u>	No progeny from ten caged pairs.	Liu (1954)
<u>P. maniculatus</u> <sup>1</sup> X <u>P. oreas</u>	No results.	Sheppe (1961)
<u>P. maniculatus</u> <sup>1</sup> X <u>P. sitkensis</u>	No laboratory progeny.	Thomas (1972)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Progeny from 1 of 23 caged pairs. F <sub>1</sub> large sized. Died soon after birth.	Watson (1942)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Viable F <sub>1</sub> from 22 of an unknown number of caged pairs. Some F <sub>1</sub> fertile in backcrosses.	Blair and Howard (1944), Blair (1944)
<u>P. polionotus</u> X <u>P. maniculatus</u>	F <sub>1</sub> progeny from 10 of 64 caged pairs. Placentas large, prenatal mortality of F <sub>1</sub> common.	Liu (1953a, 1953b)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Ten of 99 caged pairs produced liveborn. F <sub>1</sub> average larger than either species birth to adult. Maternal and F <sub>1</sub> fetal mortality high. F <sub>1</sub> fertile in both sexes.	Dawson (1965, 1966, 1971) Dawson et al. (1982)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Live born progeny four of 35 pairs. 16 near term conceptuses collected from six matings. F <sub>1</sub> placentas large (6X reciprocal) and vesiculate.	Rogers and Dawson (1970)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Eight of 12 caged pairs pregnant. 14 living near-term embryos collected. Fetal and placental weights average more than either species.	Maddock and Chang (1979)
<u>P. polionotus</u> X <u>P. maniculatus</u>	In vitro fertilization. 101 normal and 26 abnormal fertilizations of 170 ova examined.	Fukuda et al. (1979)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Seven pregnancies in test of progesterone effect.	Bell and Dawson (1983)
<u>P. polionotus</u> X <u>P. maniculatus</u>	Near-term F <sub>1</sub> from four matings collected immunosuppression study.	Bell et al., (1983)
<u>P. oreas</u> X <u>P. maniculatus</u>	Eleven caged pairs. No progeny. Mass mating (7 <u>P. oreas</u> X 4 <u>P. maniculatus</u> ) three females produced liveborn, one survived. F <sub>1</sub> growth retarded. Male sterile.	Liu (1954)

<sup>1</sup>Female in cross not given.

## C O N T R I B U T I O N S

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A few comments have been received from those of you who have had problems similar to those experienced by us when our animal facilities were undergoing renovation. I still believe that the issue of when a particular laboratory group of wild animals can be considered as a "laboratory animal" is one which must be resolved. After all a few short years ago the white mouse was derived from a "wild stock" but now has a special status. Suggestions on how to approach this issue with government agencies would be appreciated.

One current direction of our laboratory research is to evaluate residence and turnover of radioisotopes used in the field to establish maternity. A portion of this work now indicates that some isotopes can be retained in sufficient quantity in mothers to still be detectable in third and fourth litters produced by them. If radioisotope use in the field is not monitored very closely, possible confusion of relationships could occur. As single and multiple label usage allows the maximal number of combinations to be realized, if one isotope has a different residence or transfer period then litters produced by the same female could have different isotopic identifications. That would remain unknown in the field and offspring would be misidentified. If questions of dispersal or social relationship were being evaluated then small errors in identification could result in large hypothesis testing errors. In both *P. leucopus* and *P. maniculatus* the isotopes tested so far behave in the same manner.

The spring field season will begin and we are going to be looking for small disturbance sites in the forests to try to track the fate of animals whose habitats are lost. These forced dispersants could have a wide array of fates in the system. Their fate could also have a high seasonal dependency and we will be attempting to look at this throughout the year. First questions are however quite basic, can enough of the marked animals post disturbance be relocated. If that is answered this year then the project will have some possible future.

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At the University of North Carolina Pharmacology Department, we maintain a colony of deermice, *Peromyscus maniculatus*, established from a breeding stock provided by Dr. M.R. Felder of the University of South Carolina. The unique characteristic of our colony is that we possess two strains, one containing the Alcohol Dehydrogenase (ADH) enzyme (ADH+) and one genetically deficient in ADH (ADH-). We have found, however, that ADH- deermice do eliminate ethanol at rates up to 60% of the positive strain.

This strain, therefore, yields a useful model with which the "minor" pathways of ethanol oxidation can be studied in the absence of inhibitors of ADH which could be nonspecific. In our lab, techniques have been devised to perfuse the livers of these animals. Deermouse livers are about the size of a 23mm-diameter coin and weigh from 500 to 800 mg.

Our studies have demonstrated that the ADH- deermouse oxidizes ethanol almost exclusively via catalase-H<sub>2</sub>O<sub>2</sub> generation and catalase activity.

Non-ADH pathways of ethanol metabolism have been implicated in ethanol-induced liver damage. The ADH- deermouse can be used to evaluate this hypothesis by feeding them ethanol-containing diets. Since we found chronic treatment with a high-fat diet caused an increase in ethanol metabolism in ADH- deermice, controlled experiments with low-fat diets containing ethanol would be useful to test in the future. This type of experiment would be helpful in evaluating the role of acetaldehyde produced by peroxidation of ethanol via catalase-H<sub>2</sub>O<sub>2</sub> as well as H<sub>2</sub>O<sub>2</sub> generated via peroxisomal  $\beta$ -oxidation in ethanol induced liver damage. We also plan to test the effects of physiological agents such as hormones and intracellular calcium on peroxisomal  $\beta$ -oxidation.

This discussion has merely highlighted a few examples of the way we use this genetically deficient deermouse in our research. The range of possible applications of the *Peromyscus maniculatus* make it a useful animal model for the study of alcohol induced toxicity and disease.

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**Borrelia burgdorferi infection of Peromyscus leucopus.**

In the course of trapping in order to start a small breeding colony of *P. leucopus*, I noticed some severe motor problems, including ataxia, circling, lack of balance and tremor, and tetanus or chronic contraction of the rump and hind muscles. These symptoms were seen in approximately 5% of the mice captured, and appeared after a variable length of captivity, usually greater than a month. Some mice eventually succumbed and others survived. Lengthy pathological testing carried out by our Research Animal Resources Center ruled out numerous viral agents. Dr. Elizabeth Burgess of the Veterinary Medicine Department screened serum and found the antibody to the *Borrelia* spirochaete, the causative agent of Lyme disease in humans. She subsequently isolated the spirochaete from brain tissue of affected mice.

The epidemiology of Lyme disease in humans, and the distribution of *Borrelia burgdorferi* in *Peromyscus leucopus* (thought to be the natural reservoir population), in other small mammals and in domestic animals, and the distribution of the tick vector (*Ixodes* spp.) are currently under investigation in Wisconsin and elsewhere. The borreliosis in *P. leucopus* captured here in Dane county (southern Wisconsin, where Madison is located) is of interest because infected mice came from areas where no tick vectors have been seen and because there has been no report of the symptoms of borreliosis in naturally infected mice. I am interested to hear if any other workers have tested for the antibody to *Borrelia* in *P. leucopus* elsewhere in the country, especially outside of the areas of focus of Lyme disease in humans. Also of interest are any other observations of similar motor problems in *P. leucopus*. These findings indicate that some caution should be taken when handling *Peromyscus leucopus*, if there is any suspicion of infection with *Borrelia burgdorferi* which is a human pathogen.

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Case reports from the medical literature indicate that heavy consumption of alcoholic beverages may endanger acute and subacute poisoning by the industrial solvent 1,4-dioxane (1).

In our experiments, the oral toxicity of 1,4-dioxane to Wistar rats and NMRI mice was markedly increased upon prior i.p. administration of the ADH inhibitor 4-methylpyrazole (4-MP; 100 mg/kg, dissolved in phosphate buffer solution). No signs of toxicity were recorded in rats receiving 3000 mg/kg dioxane or, respectively, NMRI mice receiving 1000, 2000 and 3000 mg/kg dioxane by gavage or 4-MP alone. Unspecific signs of toxicity after single or repeated oral administration of 1,4-dioxane (1 x 3000 mg/kg or 2 x 3000 mg/kg or 4 x 1000 mg/kg or 4 x 2000 mg/kg) were much more pronounced in Wistar rats pretreated with 4-MP and subsequent application of 1,4-dioxane at identical doses. In NMRI mice similar effects were recorded at 2000 mg/kg dioxane with and without prior 4-MP treatment.

In contrast, ADH<sup>F/F</sup> and ADH<sup>N/N</sup> deermice (*P. maniculatus*) (3) did not show any toxic effects after 4 oral administrations of up to 3000 mg/kg at 4 consecutive days. After three administrations of 5000 mg/kg on consecutive days unspecific toxic symptoms and mortalities occurred. No difference in toxicity could be detected between ADH<sup>N/N</sup> and ADH<sup>F/F</sup> animals.

The results of the study indicate that in NMRI mice and Wistar rats ADH may be involved in the clearance of a toxic metabolite (possibly dehydrogenation of 1,4-dioxane-2-ol to 1,4-dioxane-2-one (2)), while in *P. maniculatus* different metabolic pathways (3) may exist for the oxidation of 1,4-dioxane to the urinary excretion products 1,4-dioxane-2-one and its open chain form  $\beta$ -hydroxyethoxyacetic acid.

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Gunn and Greenbaum recently showed that *Peromyscus oreas* and *P. maniculatus austerus* are specifically distinct (J. Mammal. 1986 67:294). These two forms are sympatric in forests on the west slope of the Cascades north of the Columbia River and in parts of the Olympic Peninsula. The extreme morphological similarity (individuals can be unequivocally identified karyotypically) and the apparent ecological similarity of the species led us to begin more detailed investigations of food habits and microhabitat selection. We established a live-trapping grid in forest habitat that ranged from nearly pure Douglas fir forest to nearly pure deciduous forest. Live-trapping data indicated similar densities of both species. Both species were captured in all macrohabitat types. We followed the movements and quantified microhabitat selection of both species with radiotelemetry. Preliminary analyses indicate extensive overlap between the two species. *P. oreas* shows a slightly greater tendency toward arboreality. We are currently analyzing stomach contents of both species from extensive collections along the west side of the Cascades. Results thus far indicate extensive overlap in food habits as well.

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We are using *Peromyscus* as model organisms to test genetic processes of importance to endangered species propagation and management. We currently maintain stocks of *P. leucopus noveboracensis*, *P. l. texanus*, *P. polionotus leucocephalus*, *P. p. niveiventris*, *P. p. phasma*, *P. p. rhoadsi*, *P. p. subgriseus*, and *P. gossypinus palmarius* for studies of inbreeding and hybridization.

We are in the final stages of a 4-year study, first initiated by Bruce Brewer (then at Cornell University), comparing the severity of inbreeding depression to initial levels of genetic variability as detected by starch gel electrophoresis of tissue proteins. Moderately inbred mice have been produced (inbreeding coefficients up to .7 for *P. leucopus* and *P. polionotus niveiventris*), and stocks differ markedly in their responses to inbreeding. We have monitored litter size, juvenile mortality, and weights at weaning, and we are beginning to examine bilateral asymmetry in skeletal measures. No relationship between the initial genetic variability of a stock (low in *P. p. phasma* and *P. p. leucocephalus*; high in *P. leucopus* and *P. p. subgriseus*; intermediate in the others) and the severity of, or the traits affected by, inbreeding depression has yet been observed.

We have also begun a study of hybridization between various species and subspecies of *Peromyscus*. We intend to monitor reproductive performance of all pairwise crosses, and then to examine skulls and legbones for asymmetry and developmental abnormalities in first and later generation hybrids.

Excess mice from our lab stocks can be made available to other researchers, though availability will vary over time. The origins of the stocks are as follows:

Species	Collecting Locality	Date lab stock established
<i>P. leucopus texanus</i>	Brewster Co., TX	1984
<i>P. l. noveboracensis</i>	Ithaca, NY	1984
<i>P. l. noveboracensis</i>	Cook Co., IL	1987
<i>P. p. leucocephalus</i>	Santa Rosa Is., FL	1984, 1988
<i>P. p. niveiventris</i>	Canaveral Nat. Seashore	1984, 1988
<i>P. polionotus phasma</i>	Anastasia Is., FL	1984
<i>P. polionotus rhoadsi</i>	Lake Placid, FL	1984, 1988
<i>P. polionotus subgriseus</i>	Ocala Nat. Forest, FL	1984, 1988
<i>P. polionotus subgriseus</i>	Withlacoochee St. Forest	1984, 1988
<i>P. gossypinus palmarius</i>	Lake Placid, FL	1987

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I have just completed a study of geographic variation in 20 non-metric cranial and post-cranial skeletal traits of *Peromyscus maniculatus*. To my knowledge, this is the first study of non-metric traits of wild caught *P. maniculatus*. I examined *P. maniculatus* collected from six locations in northcentral Kansas. Two of the sites were in cultivated valleys and four were in grazed native prairie. The cultivated areas studied appear to be higher quality habitats for *P. maniculatus* than native prairie, they support higher densities of *P. maniculatus*, individuals weight more and are larger, and reproduction begins at an earlier age.

For each population sampled, the frequencies of each of the traits were tested for sex and side dependencies. Two traits in females and only one trait in males exhibited different frequencies on the left side of the skull than on the right side. Five of the traits examined were significantly affected by sex, but only one trait was sexually dimorphic in all six populations examined. Differences in habitat quality influenced the frequency of several of the fusional traits examined, but did not effect left-right side asymmetry.

Interpopulational trait frequency differences were examined, and concordance between the phenetic distance and the spacial proximity of populations was noted. Foramenal trait frequencies do not appear to be influenced by habitat quality. Because many non-metric traits may be adaptively neutral, frequency differences between populations may result from genetic drift, thus reflecting the extent to which separate populations are isolated breeding units.

In order to further investigate the nature of these traits in *P. maniculatus*, I established a laboratory colony of *P. maniculatus* from two of my study sites; one cultivated and one native prairie. Pedigrees were kept on progeny resulting from crosses between individuals from the same original population. The offspring were sacrificed at 4 and 6 months of age. Skeletons of the parents and progeny have been prepared. I have not yet examined these individuals, but hope to within the next few months. The results of this laboratory study will be used to further evaluate the utility of non-metric traits in understanding microevolutionary divergence among populations of *P. maniculatus*.

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**Li-Hsien Lin - Ph.D. candidate and E. B. Pivorun (NIH support):**

A paucity of information exists on the physiology and endocrinology of daily torpor in rodents. This thermoregulatory response may represent a physiological state intermediate between sleep and hibernation. An understanding of the physiological and endocrinological basis/bases for daily torpor may lead to a better understanding of sleep and the mechanisms that enable the gradual, controlled entry of mammals into hibernation.

Computerized radiotelemetry is being used to monitor and quantify the torpor patterns of Peromyscus maniculatus displaying spontaneous and ration induced daily torpor bouts. The role of the opiates and the brain monoamines in modulating daily torpor has been investigated through the use of specific agonists or antagonists to these neuroendocrine factors. Alterations in torpor patterns are monitored via telemetry. Serotonin has been found to exert an stimulatory on the daily torpor response, dopamine has been found to inhibit the torpor response. High pressure liquid chromatography (HPLC) with electrochemical detection, is currently being utilized to monitor titers of biogenic amines and metabolites in discrete areas of the brain, including the hypothalamus, the pineal, the caudate putamen, the suprachiasmatic nucleus, and the medium raphe nucleus. Changes in the turnover rates of the various biogenic amines in these discrete brain areas are also being studied through the use of living brain sections to compare the neuroendocrinological state of discrete brain nuclei or regions during torpor and normothermia.

**Linda Wang - Ph.D. candidate:**

Linda's research seeks to determine the heritability of ration-induced daily torpor in the cloudland deermouse, Peromyscus maniculatus nubiterrae. Torpor is evaluated in parents and offspring using surgically implanted temperature sensitive transmitters with a computerized electronic data acquisition system. This system allows torpor parameters to be treated as continuously variable traits; therefore, standard quantitative genetics techniques can be employed in the statistical analysis. Linda is also investigating a mutant coat color. This mutant appears to be a one locus recessive allele. The affected mice lack pigment except for black pigmentation of the ears and a brown mane.

**William Yenke - Ph.D. candidate:**

The pineal has been implicated as the entrainer of circadian rhythms involving mammalian thermoregulation and torpor states. The deermouse, Peromyscus maniculatus, when faced with winter food scarcity and cold ambient temperatures, enters a torpid state. Understanding the neurochemical and physiological events involved in daily torpor is one of the research efforts of this laboratory. Bill's research attempts to understand some of the ultrastructural manifestations of torpor by a morphometric analysis of pineal tissue cultured under states of activation and inactivation. The pineals of deermice killed under various physiological states (eg., torpid, euthermic, day, night) were divided into symmetrical sagittal sections. One half of each pineal of a treatment group was cultured in a standard medium. The matching half was maintained in medium containing norepinephrine. The cultured tissue was prepared for transmission electron microscopy and photographed. The resulting enlarged photographs were examined with a digitizing image analyzer, and the pinealocyte structure and substructure ( cytoplasmic area, nuclear area, organelle size, and number) were quantified for statistical analysis. Subsequent morphometric comparison of the activated and inactivated cells is expected to extend the understanding of the morphological and physiological functioning of the organ.

**Louis DeLuca - M.S. student:**

Two approaches have been taken to assess the role of protein restriction on seasonal torpor of Peromyscus maniculatus. One study was designed to permit self-selection of dietary protein levels under conditions of either 12°C and short photoperiod or 23°C and long photoperiod. A second experiment assessed the incidence of torpor in mice fed *ad lib* on either a protein-free diet of adequate caloric density or on an isocaloric diet of normal protein content. These mice were housed in a 12°C cold chamber (8L:15D) to facilitate torpor, and temperature sensitive telemeters were used to measure core body temperature.

Preliminary results in the selection experiment indicate a significant interaction between sex and treatment for protein selection. Male deermice select a low protein level at 12°C and a high one at 23°C; females display an opposite trend. The telemetry experiments have not yielded a clear difference in torpor proclivity under the two dietary regimens.

**Linda Eldredge - M.S. student:**

Because latitudinal differences exist with respect to photoperiodic dependence (southern latitude subspecies rely less on photoperiodic cueing than their northern counterparts), a cross latitudinal study was initiated to compare the effects of photoperiod and melatonin administration on hypothalamic neuroendocrine factors in deermice from northern (PA) and southern (NC) populations. Preliminary HPLC work has been carried out to determine the effects of melatonin injections on hypothalamic biogenic amine levels in new born deermice subjected to control or melatonin injections. Linda is primarily interested in the effects of melatonin on hypothalamic dopamine levels. Dopamine is considered to be the prime inhibitory factor of pituitary prolactin production and/or release. Preliminary results indicate that differences may exist between the control and melatonin injected groups with respect to hypothalamic neurotransmitter and metabolite titers. Further work will include immunohistochemistry and radio immunoassay (RIA) procedures on pituitary tissue to determine the effect of melatonin and photoperiod manipulations on the pituitary prolactin titers.

**Mary Strayer - M.S. student:**

A cross latitudinal study was initiated to examine and compare seasonal and photoperiod effects on growth, maturation, and thermogenic capacities of Peromyscus maniculatus from a northern latitude site (Pennsylvania) and a southern latitude site (North Carolina). Animals were randomly assigned to photoperiod treatments of either 14L: 10D or 10L:14D. Weights, pelage and sexual stages were then recorded. Maximum aerobic metabolic capacities were appraised by oxygen consumption measurements using paramagnetic oxygen analyses. Brown fat metabolism was also estimated. A compatible field study on the North Carolina population accompanied this work.

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BEHAVIORAL ECOLOGY OF PEROMYSCUS AT THE  
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We are continuing the eight-year study of *Peromyscus leucopus* at the Mountain Lake Biological Station in southwestern Virginia. After reaching a peak population density of 38 mice/ha in 1981, the densities crashed to a low of less than 6 animals/ha in 1983 and then peaked again at 38 animals/ha in 1986. In 1987, the density reached an all time low of 5.2 mice/ha. Densities of *Peromyscus maniculatus*, which have paralleled those of *P. leucopus* were also at their lowest density of 1.6 mice/ha. The reason for the rapid decline in densities from 1986 to 1987 is not known.

The main objective of our study in 1987 was to determine if, and under what conditions infanticide occurs in *P. leucopus*, and which sex and age group commits infanticide. Secondly, we are testing the hypotheses that (1) males commit infanticide to increase mating opportunities, (2) females commit infanticide to compete for resources (nest sites, food, or territories), or (3) infants are killed and eaten for food. The study is being conducted in the field by placing pups in specially designed nest boxes within the home ranges of known animals. The age, sex, and residency (or immigrant) status of mice entering the nest boxes are monitored. Preliminary results suggest that infanticide is more common among females than among males and results from competition for resources. Male infanticide is less common probably because of the promiscuous mating system which results in confusion of paternity. It appears that a male's prior association with females inhibits infanticide. Males that had not sired litters within the previous 30 days were more prone to committing infanticide than were males that had mated. Few pups were eaten suggesting that food is not the prime motivation for killing pups.

We are now conducting a laboratory study at Villanova University to determine if cohabitation and/or copulation are sufficient to inhibit infanticide in males, and if so, for how long. Cohabitation alone does not inhibit infanticide, but copulation does. Tests are now in progress to determine the duration of the inhibitory effects of copulation, whether males recognize their own offspring or not, and if the tendency to commit infanticide is inherited. The laboratory studies are designed to corroborate our field observations. Both studies are scheduled for completion in Autumn 1988.

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