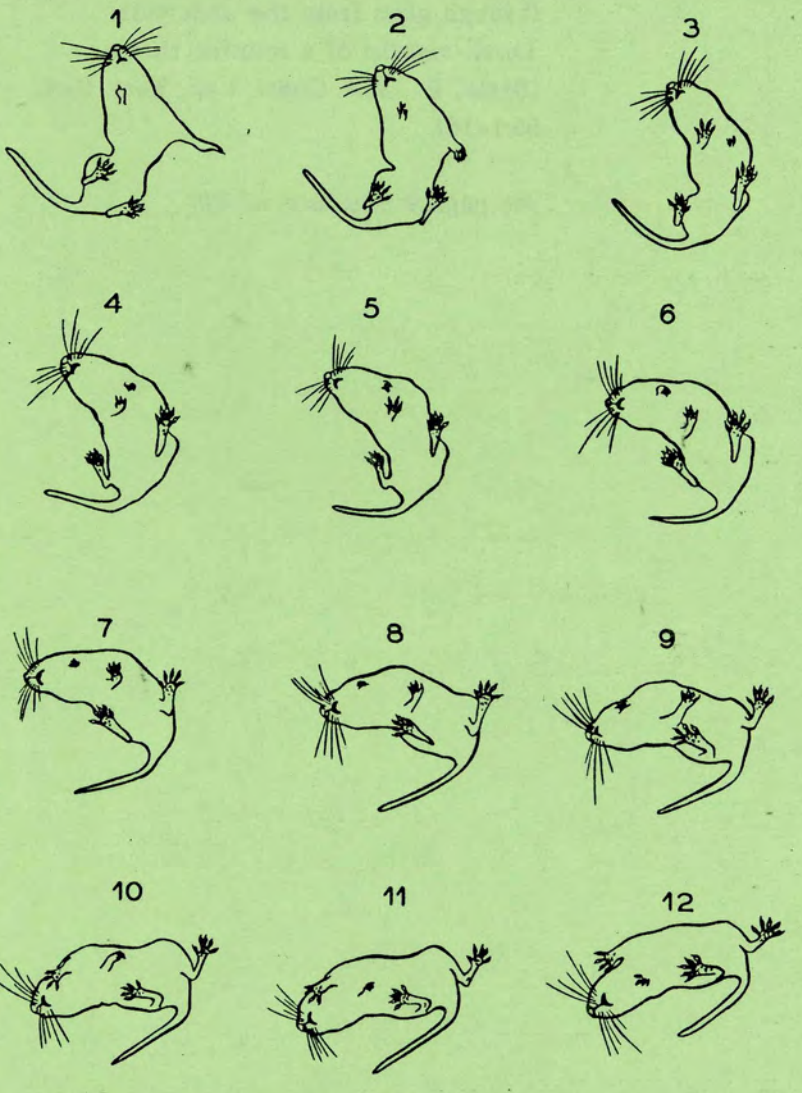
PEROMYSCUS NEWSLETTER

NUMBER TWELVE



SEPTEMBER 1991

COVER: Behavior of the "spinner" mutant *Peromyscus polionotus* drawn from consecutive frames of a movie made through glass from the underside. Three-eighths of a rotation shown. (Barto, E. 1954. Contr. Lab. Vert. Biol., 66:1-16).

See page 9 this issue of **PN**.

In PEROMYSCUS NEWSLETTER Number 12 - - -

* * * Revised and updated tables of genetic loci of *P. maniculatus*. The new list incorporates recommendations of the Genetic Advisory Committee to make the deer mouse genetic nomenclature as nearly consistent with that of house mouse (*Mus*) as possible. The nomenclatural guidelines are given on page 16. *The Journal of Heredity* now accepts only names and symbols which comply with these guidelines.

* * * An introduction to "waltzing" and "whirling" mutants of *Peromyscus*. Sue Van Ooteghem and Barbara Brown discuss the history and behavior of these genetic variants on pages 9-11.

* * * Walter E. "Howdy" Howard, our featured "Peromyscus Pioneer". A brief biography of Dr. Howard enumerating some of his many accomplishments is found on pages 12-15. We thank Rex E. Marsh of UC-Davis for generously providing us with background material. Marsh and Howard collaborated on numerous projects during a period of over twenty-five years.

* * * Entries from our readers and Recent Literature citations.

We continue to encourage entries for the "Contributions" section. The ultimate success of **PN** depends on its use as an informal forum for *Peromyscus* researchers. Please consider sending us your update before the next issue. We will mail a reminder. Deadline for PN # 13 is **February 15, 1992.**

WDD

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Genetic Loci in *Peromyscus*

Table 1 A - D *P. maniculatus* 17

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Recent Peromyscus Literature 38

* * *

P. leucopus appeared on the **Today Show** on September 6th with Jim Fowler in a feature on Lyme disease.

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We understand that **Dr. Bryan Glass** (715 S. Willis, Stillwater OK 74074) now has etched glassware featuring Peromyscus. Many mammalogists and ornithologists are familiar with his etched renderings of mammals and birds. For many years, while a faculty member at Oklahoma State, Dr. Glass was prominent in affairs of the American Society of Mammalogists.

* * * * *

We received a nice letter from **Harold Egoscue**, who was "Peromyscus Pioneer" for our March 1991 issue. He reports that he attended the graduation of his oldest daughter from college at San Diego. He was looking forward to returning to his flea research during the summer. We wish to correct an error in our March "Pioneer" sketch: the child he and his wife lost in infancy was a son. We regret the mistake in our account.

David Ribble presented a featured paper at the annual mammalogists (ASM) meetings at Kansas State in June. His paper on "The monogamous mating system of **Peromyscus californicus** *as revealed by DNA fingerprinting" was in competition for a student honorarium.*

-----and-----

speaking of the ASM meeting, at least 22 presentations (papers and posters) were centered on *Peromyscus* as indicated by the title.

* * * *

Dr. Irwin Gelman is CALLING FOR COLLABORATORS. He needs field-trapped *Peromyscus* which show symptoms of anemia or an immunodeficiency-like disease. If you find such animals, please contact Dr. Gelman. (212) 241-3749. [See p. 27, this issue PN]

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ORLANDO SCHWARTZ, of Northern Iowa University, raises the question of how to distinguish P. leucopus and P. maniculatus by morphological criteria. The problem appears to arise frequently in certain areas of the country where they co-occur. He invites discussion of the issue - see page 32.

. . . . . .

News from the Peromyscus Stock Center:

ADDITIONAL SPECIES: We currently have limited numbers of *P. californicus, P. gossypinus, P. aztecus* and *P. melanotis*, in addition to those available for distribution (See next page). A permanent *P. californicus* stock will be established for future general distribution. We can likely fill a request from anyone needing one or two of the individual species mentioned above, but we do not have them available in large numbers.

INBRED *P. MANICULATUS*: The Stock Center recently acquired two related lines of highly inbred *P. m. bairdii* which were developed by Muriel Davisson and Cecilia Schmidt at Jackson Lab. These strains have been maintained by sib mating for 25 - 26 generations. The foundation matings are breeding successfully, and expansion matings should soon make limited numbers available for distribution. The two strains are being designated PMH8A/SC and PMH1/SC by the Stock Center. Stay tuned.

MOLECULAR BANK: The Stock Center collection of molecular probes and libraries derived from *Peromyscus* is being set up. Mr. **Michael Foster** has been appointed the technician-curator of the collection. We invite anyone who has a *Peromyscus* DNA library or a molecular probe cloned from *Peromyscus* to donate a sample to the Stock Center. We will amplify these and make them available as a resource to potential users, subject to any conditions imposed by the donator.

COLONY UTILIZATION: Utilization of the Stock Center by external researchers continues to increase. Thus far in 1991 we have filled 21 requests for a total of 544 animals, with other shipments anticipated in the next few weeks. Among the institutions we recently supplied are Johns Hopkins University Dept. of Psychology, US Fish and Wildlife Service, Smith-Kline-Beechum, Virginia Living Museum, Texas A&M College of Veterinary Medicine, Yale University School of Medicine, Northeast Missouri State University Div. of Science and Florida State University Biological Science Dept. The varying missions of these institutions reflects a broad interest in *Peromyscus*.

COLLABORATION ON COAT COLOR GENETICS: The Stock Center has acquired several coat color mutations which have never been formally described. The Stock Center is collaborating with several individuals to complete the formal genetics and enter descriptions into the literature as a series of brief reports. The first of these, on the ashy mutation, appeared last year (*J. Hered.*, 81:309ff). Others are either submitted or in preparation: "Variable white" (with K. Cowling, R. Robins and others), "Golden nugget" (with E. Horner), "tan-streak" (with L. Wang) and "California blonde" (with V.L. Roth). The mutant names are provisional, and subject to change.

LINKAGE AND MAPPING: The Stock Center has embarked on a program to expand the linkage map of *Peromyscus* utilizing interspecific hybrid backcross analysis of RFLPs, coat color and protein electrophoretic variants. Dr. Duke Rogers of BYU is a collaborator in this project and will complement the formal genetic analysis at the Stock Center with cytogenetic analysis of *in situ* hybridization.

REPRINT COLLECTION: The *Peromyscus* reprint collection continues to grow by addition of new papers as well as donations of older reprints. The are now about 1700 different reprints of publications on *Peromyscus* in our files. We will photocopy specific reprints on request. Call (803) 777-3107.

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 Research 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 fee. 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. Third to sixth generation in captivity.
P. leucopus (LL Stock)	Derived from 38 wild ancestors captured between 1982 and 85 near Linville NC. Seventh to ninth generations in captivity.
P. maniculatus X *P. polionotus* F_1 Hybrids	Sometimes available.

MUTATIONS AVAILABLE FROM THE STOCK CENTER

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 *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^W/a^W	Egoscue's "non-agouti" (Egoscue, 1971)
Wide-band agouti $A^{Nb}/-$	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.

MUTATIONS AVAILABLE FROM THE STOCK CENTER (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)
Epilepsy *ep/ep*	U. Michigan *artemisiae* stock (Dice, 1935)
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)
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.

Other Resouces of the *Peromyscus* Genetic Stock Center:

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.

Purified DNA from *P. maniculatus, P. leucopus, P. polionotus* and other species upon request.

P. maniculatus genomic library.

P. maniculatus liver cDNA library.

Several behavioral (neurological) variant deer mice held in the *Peromyscus* Behavior Genetics Stock Center at the University of South Carolina Aiken Campus. See PN #10 for additional information.

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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WHIRLING BEHAVIOR IN *PEROMYSCUS*

Suellen A. Van Ooteghem and Barbara A. Brown

The cover of this issue shows a drawing of the whirling pattern characteristic of spinner (*sp*), one of three distinct whirling mutations described in *Peromyscus* literature. For the purpose of this discussion, the term whirling applies to any subpopulation which shows a pattern of turning around briskly and repeatedly in small circles in a horizontal plane.

Two of these mutations, spinner and waltzer, are potentially extinct. Whirling behavior has, however, recently been noted in a number of different *Peromyscus* stocks currently maintained by the *Peromyscus* Stock Center. It is highly likely that these recently isolated stocks are descended from the original mutant stocks. Therefore, recent efforts by staff of the Neurological and Behavior Mutant Colony, one branch of the *Peromyscus* Stock Center, have centered on determining if the whirling stocks currently isolated represent a re-isolation of the original mutant stocks already described (if so, the mutant will then be re-established after being traced back to the original mutant stocks) or if the whirling stocks currently available have arisen *de novo*, representing new mutations.

The three mutations which have been previously described in the literature are waltzer (*v*), spinner (*sp*) and whirling in the epilepsy (*ep*) mutant stock. Each of these mutations arose in laboratory subpopulations of *Peromyscus*, and each was isolated from phenotypically normal wild-trapped populations. Genetic analyses previously established the independence of each of these three mutations. These mutations are each described briefly below.

Waltzer (*v*) individuals whirl both clockwise and counterclockwise, but sometimes are noted to whirl in only one direction. Most waltzers are identifiable by the time they are one month old, however the rate, frequency and age of onset of waltzing is somewhat variable. Vigorous sideways jerks of the head (resembling nystagmus) are seen in waltzer homozygotes. Deafness is not usually observed in waltzers until the animal is quite old.

The waltzer mutation arose in *P. maniculatus bairdi* stock trapped in Alexander, Iowa. Waltzer is reported to show linkage with the coat color mutation wideband (A^{Nb}) by 10-11 cM. Wideband is a coat color mutation which lengthens the agouti band (making the animal more yellow in appearance). This mutation also reduces the frequency of nonbanded hairs and is allelic with nonagouti. Studies are currently underway to determine if animals showing a similar phenotype can be traced back to the original waltzer stock, and to determine if the recently isolated behavior mutation which shows a phenotype similar to that of waltzer is linked to wideband.

Spinner (*sp*) individuals show whirling behavior similar to that of waltzer except that spinners become deaf at an early age. The grade of whirling and deafness varies, but little overlap with normal behavior occurs. Sideways jerks of the head are reported to be less severe in these animals than in either waltzer or epilepsy homozygotes. While variable in occurrence, these animals have been noted as displaying a sharp upward tilt of the head both during movement and when standing still or sitting. No spinner has been noted to swim on the surface of the water for more than a few strokes. Once underwater, these animals swim in an erratic course with constant twisting and turning not restricted to any one plane. These animals must be rescued or they will drown. Since an erratic swimming pattern is so characteristic of spinner but not of waltzer, the swimming ability of whirling animals isolated from our current colony stocks is being tested. Should this pattern be observed, the pedigree of affected animals will be traced, and the animals will be tested for allelism with other whirling stocks. The original spinner mutation arose from *P. polionotus rhoadsi* stock trapped near Leesburg, Florida.

Epilepsy (*ep*) causes a syndrome of whirling, sound-induced seizures and progressive deafness in homozygotes. Classification is made by determining the response of the individual to jingling keys. Homozygotes respond by whirling and/or dashing wildly around the enclosure, followed by a clonic, tonic seizure. The seizure may be followed by a period of stupor, when the animal lies limp in whatever position it is placed. Expression is variable and animals need to be classified early because they usually become completely deaf and unresponsive to sound by three to four months of age. The peripheral and central auditory pathway of the epilepsy homozygote shows marked degenerative changes.

Epilepsy homozygotes often show whirling in both directions, movement in figure eights, and rapid pivots and pirouettes. When whirling is noted in the epilepsy homozygote the animal swims poorly, and as with spinner, does not remain on the surface of the water. Once underwater, affected animals swim in three dimensional circles and figure eights. If the animal touches the bottom while swimming it immediately orients to the bottom, whirling in two dimensional circles and figure eights on the bottom surface (underwater). These animals, like spinners, must be rapidly rescued or they will drown. This mutation arose from decendants of *P. maniculatus artemisiae* trapped near Lyons Ferry, Washington. The epilepsy mutation is currently well established in our colony, and available to interested investigators.

In addition to the above-identified mutant stocks, at least two other whirling stocks are currently under investigation. One of these has been noted in a cage bred nonagouti stock descended from wild-caught *P. maniculatus gracilis* from New Hampshire. These animals turn tight circles, each animal turning in one predominant direction. Swimming behavior in these animals has not yet been tested. Work is currently underway to determine if this whirling behavior is inherited. If so,this possible linkage with nonagouti will be explored, potential allelism with any of the other currently-maintained whirling mutants will be tested.

The second new stock which shows whirling behavior is associated with a newly-recognized dominant coat color mutation, variable white. This mutation is characterized by patches of hairs which are white to the base. Variable whites also show reduced amounts of yellow pigment, giving the animal a more grey appearance overall. A more complete description of this mutation is found in the manuscript cited below, which has recently been submitted for publication.

If the ears of variable white animals are white, the animal appears unresponsive to sound and often whirls in tight circles. Swimming behavior in whirling variable white animals is markedly abnormal. These animals cannot stay on the surface of the water for more than a few seconds, and then, as noted with spinners, the individual goes underwater twisting and turning erratically, whirling and executing figure eights in three dimensions. Since these animals appear in distress almost immediately, they must be rescued. This mutation arose spontaneously in cage bred *P. maniculatus bairdi* stock maintained at Michigan State University. The stock has since been transferred to the *Peromyscus* Stock Center for continued observation and characterization.

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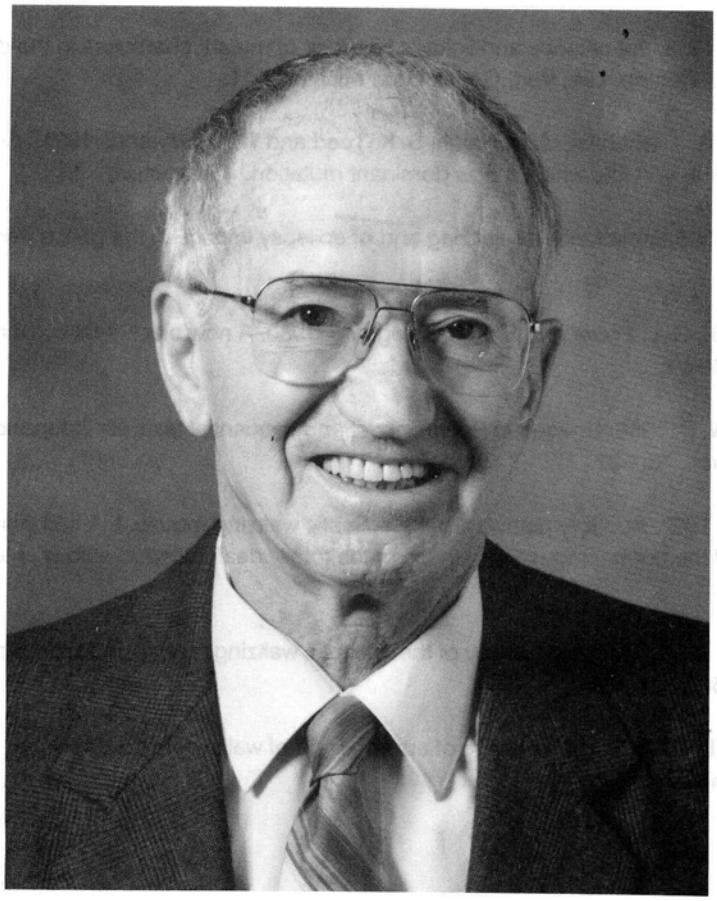

Walter E. Howard

Walter E. Howard

Walter E. "Howdy" Howard is among the outstanding "Peromyscus Pioneers" who received doctorates during the 1930's, 40's and 50's at the University of Michigan under the direction of Lee R. Dice. Howard's classic dissertation study of deer mouse dispersal and inbreeding on the George Reserve (1949. *Contrib. Lab Vert. Biol.* 43:1 ff) remains one of the underpinnings of mammalian population biology and is still cited regularly in the 1990's[1]. His innovative use of nest boxes to explore breeding structure among rodents provided some of the first sound data on inbreeding of deer mice in the wild. From his data it became possible to reasonably estimate inbreeding coefficients in this natural population. Had this been Howard's sole contribution to *Peromyscus* biology, he would have established himself as a pioneer, but this was only the beginning of a remarkable career in wildlife management and rodent population biology.

Walter Howard was born at Woodland, California, April 9, 1917. His father was a horticulture professor at the recently established agricultural college of the University of California at Davis, where Howard spent much of his youth. The area was then still rural and here young Howard, like many boys of his generation, learned to hunt and fish. He also captured wild rodents, snakes and other animals as pets. In this setting he developed an appreciation for wildlife and natural resources which continued thoughout his life. Two other notable experiences in his boyhood presaged events in his later career. He accompanied his father on European sabbaticals in 1921 and 1930 which likely whetted his subsequent enthusiasm for foreign travel.

Howard received his bachelor's degree in zoology from U.C. Berkeley in 1939, and spent a brief period pursuing graduate research at Davis in a study, directed by John T. Eurlen, Jr., of dispersal and social relationships in valley quail. About this time Howdy and Betty, now his wife of 50 years, were married. In the autumn semester 1940, Dice accepted him as a graduate student at Michigan, and he soon became the "straw boss" of Dice's lab under the immediate direction of W. Frank Blair, and shortly thereafter became a U.M. Fellow. In a collaboration with Blair (1944. *Contrib. Lab. Vert. Biol.* 26:1ff) Howard examined sexual isolation among three forms of *P. maniculatus* and *P. polionotus* using an experimental interconnected cage system in a laboratory situation. They found that *P. p. albifrons* is less isolated from *P. m. blandus* than is *P. p. leucocephalus*. Laboratory-produced interspecific hybrids were used in this study, as well. This was the first of several similarly-designed experiments conducted by Blair and others in subsequent years.

In December 1942 Howard was called to World War II service with the Ski Troops in the Aleutian Islands, and later as part of the U.S.A. Typhus Commission on the Burma Road. After more than three years of active duty, he resumed his studies at Michigan receiving his Ph.D. degree in 1947. Howard's dissertation, his famous study cited above, was published in 1949, but most of the field work had been conducted in his first two years at Ann Arbor. Using 136 nest boxes, as originally designed by A.J. Nicholson, Howard handled in excess of 1200 individual *P. maniculatus* a total of more than 4000 times. The nest boxes, which were placed at various sites on the George Reserve, thus proved to be a most effective means of tracking the deer mouse population. Each animal detected in the boxes was marked, and records maintained of pairings, litters born and numerous other data. Howard estimated that 4 to 10% of the litters produced were the product of parent-offspring or sib matings. He also found significant seasonal effects on breeding and survival, and estimated mean survival rates. Among the more interesting observations were examples of cross fostering among females and their litters which shared a nest box. Another report, co-authored with Dice (1951. *Contrib. Lab. Vert. Biol.* 50:1ff), utilized Howard's data on dispersal to document the distance traversed by individual deer mice from their birthplace to their breeding sites.

[1] *e.g.* Sharp and Millar (1990), Thompson (1990), Schug *et al.* (1991). See "Recent Publications" pp. 43-44.

Howard completed his doctorate about the same time that Blair, having recently returned to Michigan from wartime service, decided to move to the University of Texas (See **PN** #5). Dice tried to persuade Howard to remain at Michigan and assume Blair's vacant position. However, in the meanwhile, Dr. Tracy I. Storer was able to offer Howdy a position with an attractive salary at U.C.-Davis. Howard returned to Davis as an instructor in zoology and remained in various positions at the Davis Campus for the remainder of his academic career.

At Davis Dr. Howard's research became much more applied. He became well-known nationally and internationally as an authority on vertebrate pest control. As a protege of Dice, Howard had acquired an appreciation for ecology, and was early to see that a knowledge of wildlife ecology was a key to its management and control. While his work at Michigan had centered on *Peromyscus*, in his new position he necessarily broadened his work to include coyotes, bear, deer, rabbits, jays, snakes and even frogs and vampire bats. Nevertheless, rodents in the broad sense still represented a major area of expertise. Rodent pest control, particularly, became a focus of his work. He and his colleagues published numerous articles and technical reports concerning control of rodents under various circumstances. The pocket gopher populations in California were a particular source of concern to agriculture, and Howard addressed the problem with a combination of rodenticide and ecological approaches, including development of a mechanical baiting device. He also demonstrated how rodents and other small vertebrates survive fires. One interesting discovery involved *Peromyscus*. He found that deer mice exposed to sublethal doses of rodenticide remembered the experience for at least six months, and tended to avoid the bait thereafter. As a result, he recommended mixing individual lethally dosed bait seeds among untreated ones as a more effective means of control.

In 1957 Howard received a Fulbright Award to work in Australia and New Zealand, where he became deeply involved in rabbit control. This was the first of many extended foreign travels to advise on matters of vertebrate pest control. He returned to the South Pacific area in 1962-63 on a sabbatical, during which much of the time was spent in New Zealand working on deer management. From 1969 through 1979 Howard visited some 17 foreign countries, several more than once, usually under the auspices of UN-FAO or WHO, to advise on rodent and rabbit control practices. In addition to these, there were numerous other visits to third world and other countries to attend conferences and to present lectures and seminars. As an example during 1984 he spent 2 1/2 months in China presenting lectures on rodent control and ecology.

As a consequence of his background in ecology and the necessity of employing practical approaches to population control of pest species, Dr. Howard developed a philosophy which of applied ecology which is reflected in much of his research and writing, but which also provokes controversy (1976. Proc. 7th Vert. Pest Conf. p.116ff). He clearly believes that it is a given that humans will modify their own environment, and, hence, both positive and negative interactions with other species will occur. And, further, he believes that nature requires management and control where it impinges on human activity. For example, rodents which forage on crops and carnivores which prey on livestock in his opinion obviously must be restricted. Thus, Howard's approach is not whether to, but rather how to control detrimental species. Some individuals of one species, he argued, must die that others might live. Therefore, he views death as a necessary part of the cycle which assures continued life, and he certainly applied this principal to vertebrate pest control. However, recognizing this he sought the means to make the control process as humane as possible. For example, he strongly advocated chemosterilization, where feasible, as an alternative to poison for rodent control (1970. Proc. 4th Vert. Pest Conf. p.55ff. with R.E. Marsh), and where poisons were necessary, he recommended utilization of those likely to produce least distress on the animals and least damage to the environment (1970. J. Forestry 68:220ff. with R.E. Marsh and R.E. Cole). Howard's sympathies have not rested with strict preservationists, animal rights activists and those of like persuasion. Undoubtedly, this is at least partially true because he has been influenced by the dire human needs he has experienced in third world countries where rats and other pests constantly challenge the welfare of people.

While Howdy Howard is an authority on rodent population control, his concern extends to the human species, as well. Beginning with a guest editorial in *BioScience* (1968. 18:372ff) and a widely-read article, "The Population Crisis is Now", in the same journal (1969. 19:779ff), he expressed his alarm at the human population growth rate and noted the consequences were it to go unchecked. In recommendations, that, no doubt, would be unpopular in the current American socio-political atmosphere, he stated the need for government to impose compulsory contraints on reproduction. Howard felt that wealth should not be a pre-condition for the privilege to reproduce. These views were reiterated in several mid-career publications.

At Davis, Howard taught courses in "Wildlife Ecology" and "Principles of Vertebrate Control". During the 1970's his course "Population Problems: Issues in Human Ecology" attracted more than 5000 students. He has directed numerous graduate student programs, and continued to do so as Professor Emeritus. He has been active in numerous professional and civic organizations including the American Society of Mammalogists, the Wildlife Society (President of the Western Section, 1955-56), the Ecological Society of America, the Animal Behavior Society, the Society for Range Management, AIBS and AAAS. As a speaker, he has addressed the issues of animal welfare, population control and "the balance of nature".

Howdy Howard semi-retired in July 1987 and assumed the title of Professor Emeritus. Nevertheless, he has continued to direct several graduate students. As noted above, he still publishes and debates current ecological issues. He resides near the Davis Campus, bikes to his office daily, unless he is off somewhere presenting a talk or lecture. Because of time commitments, he gave up hunting and fishing some years ago. The Howards have two sons, Tom and Casey, one lives in northern California, the other in Oregon, and a daughter, Kathy, who is a teacher.

Howard authored more than 400 articles, reports, manuals, chapters and other publications during his career, many of them co-authored with his colleague Rex E. Marsh. His publication record spans 52 years - and is still going! His earliest publication dates to 1939 with J.T. Emlen on a bird census at Davis (*Bird-Lore* 42:52-53) and fifty-one years later includes 12 1990 citations, most recently a chapter with Marsh, "Vertebrate Pests", in *Handbook of Pest Control* (A. Mallis, ed. p. 771ff). While 18 of Howard's paper's deal principally with deer mice or other *Peromyscus*, many others allude to *Peromyscus* in the context of small rodents generally. By any measure, Walter E. Howard's impact on ecological and behavioral knowledge of *Peromyscus* has been enormous. Those who conduct field work with deer mice today owe him a debt of gratitude for his pioneering efforts. (WDD)

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1991. Correspondence Rex E. Marsh to WDD.

1989. Introduction of Dr. Howard to Western Section of the Wildlife Society Annual Meeting, Redding CA

1987. Letter to WDD from Walter E. Howard.

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Additional publications provided by Rex E. Marsh and from the files of the *Peromyscus* Genetic Stock Center.

GENETIC LOCI IN THE DEER MOUSE

(*Peromyscus maniculatus*)

Tables 1A, B, C and D list recognized genetic loci described in *Peromyscus maniculatus* or other species of the *maniculatus*-group. This list is limited to loci for which formal mendelian analysis has been conducted and appropriately reported in the published scientific literature, and/or for which nucleic acid sequences have been published. Additional genetic traits are known some of which have been cited in abstracts, casual reports, newsletters, grant proposals, papers presented at meetings *etc.* The latter are not included, since the descriptions and genetics are generally insufficient to formally define the loci. Presumptive loci described from natural polymorphisms in the absense of formal genetic analysis are not listed here. Protein electrophoretic and other biochemical or immunological variants known in natural populations are listed elsewhere (See **PN** # 8 pp. 14-26 and # 9 pp. 19-22).

Standardization of genetic nomenclature for *Peromyscus* is a function of the Genetic Advisory Committee for the genus. The following guidelines are applied:

1. To the maximum extent feasible *Peromyscus* genetic nomenclature and conventions will be consistent with those used for other mammalian species, particularly mouse (*Mus*). Where homology is evident or very likely, the same locus name and symbol is employed. Because homology among alleles is more difficult to ascertain, allelic symbols (superscripts) do not necessarily correspond to those of other species.

2. Dominant and incompletely dominant variant or mutant genes are designated with the first letter of the symbol capitalized. Recessive variant or mutant genes are indicated in lower case letters. The wild-type (normal or standard) allele for morphological, pelage color and behavioral traits, when recognized, is symbolized with a "+" sign. Electrophoretic allelic variants of proteins or subunits are indicated by superscripts in alphabetical sequence, except for null alleles which are designated, with an "o" superscript; or, in some cases, by relative mobility with reference to a standard mobility "100". Restriction fragment length variant alleles are are designated by a numerical sequence or size in kilobases. Distinct loci with similar phenotypic effects may be indicated in a hyphenated numerical or alphbetical series.

3. Symbols published by the original investigator are given priority, unless there is clear homology with *Mus* loci. If an original symnbol is in conflict with an established one for *Mus*, the equivalent *Mus* symbol is given preference. In cases where the original symbols have been superseded by subsequent common usage, the latter has been adopted. 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 in *Peromyscus* priority is given to the first reported, and an alternate designation is devised for the other. (In Tables 1 A-D previously published obsolete names and symbols are listed in parentheses.)

4. Presumed loci described solely on the basis of variation observed among individuals in the absence of convincing mendelian or molecular analysis are not considered firmly established, and are listed separately (See above).

5. Linkage assignments are subject to annual updates of the *Peromyscus* linkage map. The *Peromyscus* linkage map will be updated in **PN** #13.

Table 1

Genetic Loci Formally Described in the *Peromyscus maniculatus* Species Group:

A. Coat and Eye Pigmentation and Pattern Variants.

Name of locus and allelic variants	Symbol	Mode of inheritance[1]	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
AGOUTI			III			
Wide-band agouti	A^{Wb}	dominant		McIntosh (1956a)	Blair (1947) as "buff"	Clark (1938) as "buff"
White-belly non-agouti	a^{w}	recessive		Egoscue (1971)	*	
Non-agouti (Black)	*a*	recessive		Horner *et al.* (1980)	*	
ASHINESS	*ahy*	recessive		Teed *et al.* (1990)		
BROWN	*b*	recessive	II	Huestis and Barto (1934)	Blair (1947), McIntosh (1956a), Dawson *et al.* (1969)	Huestis and Barto (1934), Blair (1947), Barto (1955, 1956), McIntosh (1956a)
Orange-tan	b^{or}	recessive		Egoscue and Day (1958)		
BLONDE[2]	*bln* (*bl*)	recessive		Pratt and Robbins (1982)		
ALBINO	*c*	recessive	I	Sumner (1922)	Clark (1938)	Sumner (1922), Clark (1936, 1938), Feldman (1937), Barto (1942a), Huestis and Lindstedt (1946), Huestis (1946)
COLORLESS HAIRTIP*	*ctp*	recessive		Bowen and Dawson (1969)	Bowen (1968)	
DILUTE*	*d*	recessive	II	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	*p*	recessive	I	Sumner (1917) as "pallid"	Clark (1938), Barto (1942b)	Sumner (1922), Clark (1936, 1938), Feldman (1937), Snyder (1960a)
PLATINUM[2]	*plt* (*pt*)	recessive		Dodson *et al.* (1987)		Dodson *et al.* (1987)
RED EYE[2] (Heterochromia)	*rde* (*r*)	recessive		Huestis and Willoughby (1950)		
DOMINANT SPOT (Whiteface)	*S*	dominant		Feldman (1936)		Feldman (1937)
SILVER	*si* (*sl*)	recessive	I	Huestis and Barto (1934)		Huestis and Barto (1934), Huestis and Piestrak (1942), Huestis and Lindstedt (1946), Barto (1956)

(Table continued)

Table 1A. Coat and Eye Color Variants (Continued)

Name of locus and allelic variants	Symbol	Mode of inheritance[1]	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
WHITE CHEEK[2]	*Wck* (*Wc*)	dominant		Blair (1944)	Bowen and Dawson (1977)	Blair (1944)
WHITESIDE[2]	*ws* (*wh*)	recessive		McIntosh (1956b)		
YELLOWING[2] (Yellow)	*y*	recessive		Sumner (1917)	Sumner and Collins (1922), Clark (1938), McIntosh (1956a)	Sumner (1922), Feldman (1937), Barto (1956), McIntosh (1956a)
Complexly inherited coat pattern traits:						
Minor white spotting (Star, splash, etc.)	*p-1*, *p-2*	recessive incompletely penetrant		Feldman (1936)	Sumner (1932), Barto and Huestis (1933)	
Grizzled[2]	"*Gr*" (*G*)	"complex dominant"		Sumner (1928, 1932)		
Coat pattern in *P. polionotus*				Bowen and Dawson (1977)	Bowen (1968)	Bowen and Dawson (1977)
Pointed A[2]	*Pt-A* (P_A)	dominant	VII			
Pointed B[2]	*Pt-B* (P_B)	dominant	VII			
Tapered[2]	*Tpt* (*Tp*)	dominant				
Coat pattern modifiers				Bowen and Dawson (1977)		
Squared modifier[2]	*Msq* (*Rs*)	incompletely dominant				
Tapered modifier[2]	*Mtp* (*Rt*)	dominant				

B. Integumentary, Skeletal and Pathological Variants.

Name of locus	Symbol	Mode of inheritance[1]	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
CATARACT-WEBBED[2] (Syndactyly)	*cwb* (*cw*)	recessive		Anderson and Burns (1979)		
FLEXED TAIL	*f*	recessive	1	Huestis and Barto (1936a)		Huestis and Barto (1936a), Huestis and Piestrak (1942), Huestis and Lindstedt (1946), Huestis *et al.* (1956), Barto (1956)
HAIRLESS-1	*hr-1*	recessive		Sumner (1924)		Sumner (1924, 1932), Feldman (1937), Clark (1938), Barto (1942a, 1955, 1956), McIntosh (1956a)
HAIRLESS-2	*hr-2*	recessive		Egoscue (1962)	Knapp and Dawson (1991)	
NUDE*[2] (Post-juvenile nude)	*nd* (*n*)	recessive		Clark (1938)	Barto (1942a)	
SPHEROCYTOSIS (Inherited jaundice)	*sph*	recessive		Huestis and Anderson (1954)	Huestis *et al.* (1956), Motulsky *et al.* (1956)	Huestis *et al.* (1956)

C. Behavior and Neurological Variants.

Name of locus	Symbol	Mode of inheritance[1]	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
BOGGLER[2]	*bgl* (*bg*)	recessive		Barto (1955)	Vandermeer and Barto (1969)	Barto (1955)
EPILEPSY[2] (EP; waltzing in *artemisiae*)	*epl* (*"e"*, *ep*, v_2)	recessive		Dice (1935)	Clark (1938), Watson (1939), Chance and Yaxley (1950), Barto (1954, 1956)	Watson (1939), Barto (1956)
JUVENILE ATAXIA[2]	*jtx* (*ja*)	recessive		Van Ooteghem (1983)		
SPINNER*[2] (Waltzing in *rhoadsi*)	*spn* (*sp*, v_3)	recessive		Watson (1939)	Barto (1954)	
TREMOR*	*tr*	recessive		Huestis and Barto (1936b)		
WALTZER* (Waltzing in *bairdii*)	*v* (*w*)	recessive	III	Dice (1935)	Clark (1938), Watson (1939), Dice *et al.* (1963)	Barto (1942a, 1954, 1956), McIntosh (1956a)

D. Biochemical and Immunological Variants.

Name of locus	Allelic designation	Linkage group	Definitive 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 *et al.* (1983)
ALBUMIN (serum)	*Alb*^{100} *Alb*^{96} *Alb*^{86}	VI	Brown and Welser (1968), Jensen and Rasmussen (1971)	Dawson (1982), Dawson *et al.* (1983)
AMYLASE (salivary)	*Amy-1*^{a} *Amy-1*^{b} *Amy-1*^{c}	VI	Evans *et al.* (1977)	Dawson *et al.* (1983)
ERYTHROCYTIC ANTIGEN	$Ea^A = (Pm^A)$ $Ea^B = (Pm^B)$ $Ea^C = (Pm^C)$	IV	Rasmussen (1961), Savage and Cameron (1971)	Randerson (1973)
ESTERASE (erythrocytic)[2]	*Es-3*^{o} (*Es-1*) *Es-3*^{a} *Es-3*^{b} etc.	IV	Randerson (1965), Van Deusen and Kaufman (1978)	Randerson (1973)
ESTERASES (tissue and serum)	*Es-1* through *Es-7* (Symbols not standardized)	VIII	Rasmussen and Jensen (1971), Dawson (1982), Gill (1976), Baccus *et al.* (1980)	Dawson (1982)
GLYCEROL-3-PHOSPHATE DEHYDROGENASE[2] (tissue)	*Gdc-1*^{a} (*Gpd-1*) *Gdc-1*^{b}		Gill (1976)	
GLUTAMATE OXALOACETATE TRANSAMINASE (soluble) (ASPARTATE AMINO TRANSFERASE)	*Got-1*^{a} *Got-1*^{b} *Got-1*^{c}		Gill (1976)	Dawson *et al.* (1983)

(Table Continued)

Table 1D (Continued)

Name of locus	Allelic designation	Linkage group	Definitive description and formal analysis	Recombination reported
GLUCOSE-6-PHOSPHATE (AUTOSOMAL HEXOSE-6-P) DEHYDROGENASE[2] (soluble)	*Gpd-1*^{a} (*G6pd-1*) *Gpd-1*^{b}		Shaw and Barto (1965), Shaw (1966)	
HEMOGLOBIN - ALPHA TYPE GLOBINS (Duplicated locus)	*Hba*^{1} = (*Hb*^{1}) = (*Hbl*^{a}) *Hba*^{2} *Hbc*^{o} = (*Hb*^{o}) = (*Hbl*^{a}) *Hbc*^{1} *Hbc*^{2} = (*Hb*^{1})		Thompson *et al.* (1966), Rasmussen *et al.* (1968), Jensen *et al.* (1976), Maybank and Dawson (1976), Snyder (1978, 1980b)	
HEMOGLOBIN - BETA TYPE GLOBINS (triplicated locus)	*Hbb*^{1} *Hbd*^{a} *Hbb-b1* *Hbd*^{1} or *Hbb-b2* *Hbe*^{a} *Hbb-b3* *Hbe*^{1}	I	Snyder (1978, 1980b), Padgett *et al.* (1987)	Snyder (1980a)
HAPTOGLOBIN (serum)[2]	*Hp*^{1} (*Hpf*) *Hp*^{2}		Rasmussen (1968), Griswold and Dawson (1971)	
IMMUNOGLOBIN ($7Sy_1$)	*Ig*^{f} *Ig*^{l}		Coe (1972)	
LEUCINE AMINOPEPTIDASE (serum)	*Lap-1*^{a} *Lap-1*^{b}	V	Dawson (1982)	Dawson (1982), Dawson *et al.* (1983)
LACTATE DEHYDROGENASE[2] A SUBUNIT (tissue)	*Ldh-1*^{a} (*Ldh-A*) *Ldh-1*^{b}		Cattanach and Perz (1969)	
LACTATE DEHYDROGENASE[2] B SUBUNIT (tissue)	*Ldh-2*^{f} (*Ldh-B*) *Ldh-2*^{s}		Shaw and Barto (1963)	
6-PHOSPHOGLUCONATE DEHYDROGENASE (tissue)	*Pgd-1*^{a} *Pgd-1*^{b}		Gill (1976)	Dawson *et al.* (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)	
SUPEROXIDE DISMUTASE	*Sod-1*^{j} = (*Ng*) *Sod-1*^{p} *Sod-1*^{m}		Birdsall *et al.* (1970)	
TRANSFERRIN (serum)	*Trf*^{a} = (*Trf*^{1}) *Trf*^{b} *Trf*^{f} *Trf*^{s} *Trf*^{m} = (*Trf*^{M})	V	Rasmussen and Koehn (1966), Biggers and Dawson (1971), Griswold and Dawson (1971), Canham *et al.* (1970)	Dawson (1982), Dawson *et al.* (1983)

*Probably extinct in laboratory stocks.

[1]Autosomal unless otherwise stated.

[2]Symbols changed to avoid confusion with those in laboratory mouse (*Mus*). Obsolete published symbols shown in parentheses.

GENETIC LOCI IN SPECIES OF *PEROMYSCUS* OTHER THAN DEER MOUSE

Most formal genetic analysis in *Peromyscus* has been conducted in the deer mouse (*P. maniculatus*). However, a very limited number of genes have been formally described in other species. Seven loci have been identified in the white-footed mouse (*P. leucopus*) which are listed in Table 2. Three other variant loci have been described in miscellaneous species and are listed in Table 3.

Table 2

Genetic Loci Formally Described in the *Peromyscus leucopus* Species Group

Name of locus	Symbol and alleles	Mode of inheritance[1]	Reference	Recombination reported
ALBINO	c	recessive	Castle (1912)	
CARBONIC ANHYDRASE	Ca^f Ca^s	co-dominance	Wilmot and Underhill (1972)	
CATALASE	Cs^a Cs^b	co-dominance	Jensen (1969)	
ESTERASE-3 (Esterase-1)[2] (erythrocytic)	$Es\text{-}3^0$ ($Es\text{-}1^a$) $Es\text{-}3^b$	semi-dominant	Wilmot and Underhill (1973)	
ESTERASE-2 (serum)	$Es\text{-}2^0$ ($Es\text{-}2^a$) $Es\text{-}2^b$	semi-dominant	Wilmot and Underhill (1973)	
HEMOGLOBIN	Hb^A (in *P. gossypinus*) Hb^B (in *P. gossypinus*) Hb^C (in *P. gossypinus*) Hb^D (in *P. leucopus*)	co-dominance	Foreman (1966)	
MAJOR HISTOCOMAPTIBILITY COMPLEX	*Mhc* (Classes I, II; multiple haplotypes)		Crew *et al.* (1989, 1990)	

[1] All are autosomal.

[2] Name and symbol changed to correspond to *Mus*. Obsolete names and symbols in parentheses.

Table 3

Formally Described Genetic Loci in Miscellaneous *Peromyscus* Species

Species	Locus	Symbol and alleles	Mode of inheritance	Reference
P. truei	ESTERASE-1	$Es\text{-}1^{100}$ $Es\text{-}1^{93}$	co-dominance	Zimmerman and Kilpatrick (1975)
P. eremicus	PECTORAL SPOT	*psp*	recessive	Huestis (1925) Clark (1938)
P. californicus	HAIRLESSNESS	*hm*	recessive ?	Packchanian and Louis (1964)

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NOTICE

PEROMYSCUS NEWSLETTER IS NOT A FORMAL SCIENTIFIC PUBLICATION.

Therefore ...

INFORMATION AND DATA IN THE "CONTRIBUTIONS" SECTION SHOULD NOT BE CITED OR USED WITHOUT PERMISSION OF THE CONTRIBUTOR.

THANK YOU !

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Genes of major histocompatibility complexes (MHCs) encode highly polymorphic antigen binding molecules (class I and II antigens) which have been linked to disease susceptibility, reproduction, aging, and a variety of other physiological processes. The evolution of MHC gene polymorphism and class I and II multi-gene families is intriguing and currently subjects of considerable controversy. We have ventured in this field via the molecular analysis of the *Peromyscus leucopus* MHC which has now been termed *Pele*.

Pele class II gene loci appear quite similar to those of *Mus* MHC (*H-2*) though have not been intensively analyzed (*Immunogenetics* 30:214, 1989). While *Pele* class I gene loci clearly homologous to each of the major groups of *H-2* loci have been cloned and identified (*Immunogenetics* 32:371, 1990) the degree of complexity appears far greater for *Pele* class I genes versus *H-2* class I genes. It seems that many *Pele* class I loci have expanded relative to their *H-2* counterparts with the net result being that there are at least twice as many class I loci in *P. leucopus* than in any species of *Mus* examined. Analysis of *Pele* class I genes also gave us an insight into the evolution of all mammalian class I genes, namely that short-tract DNA duplications in the middle of transmembrane domain-encoding exons is a re-occuring feature of MHC class I gene evolution (*PNAS* 88:4666, 1991).

Finally, for several reasons we cloned and sequenced the tumor necrosis factor gene from *P. leucopus* (*Immunogenetics*, in press) which lies within the MHC in mice and humans and probably most mammals. A point of general interest: using this data and assuming a silent substitution rate of about 0.9% per million years (Myr), *Peromyscus* diverged from *Rattus* and *Mus* approximately 42-52 Myr ago.

Currently we are continuing our analysis of *Pele* class I and II genes and in particular, trying to ascertain the relationships between *Pele* and *H-2* class I loci and indentify the *Peromyscus* major transplantation antigens. Collaborative efforts with Holly Wichman (U. of Idaho) and Robert Baker (Texas Tech) may yield other fruitful avenues to explore.

* * *

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DNA HYBRIDIZATION PROVIDES INFORMATION ON RELATIONSHIPS WITHIN *PEROMYSCUS*

DNA-hybridization distances were measured among seven species of *Peromyscus* and three outgroups: *Peromyscus leucopus*, *P. boylii*, *P. mexicanus*, *P. crinitus*, *P. (Podomys) floridanus*, *Onychomys leucogaster*, *Reithrodontomys fulvescens*, and *Neotoma albigula*. Thermal stability of inter-species DNA duplexes indicate genome-wide sequence similarity between the two species being compared. The reduction in stability of inter-species hybrids relative to homologous hybrids is expected to track average sequence divergence. Depressions in median and modal thermal-stability were analyzed by least-squares tree-fitting to generate trees with branch lengths proportional to amount of change. No vacillation in cladistic relationships was seen upon bootstrapping and jackknifing, except in the basal trichotomy (see below). The best-fit additive trees explain most of the variation in the observed distances, while fitting trees to randomized distance matrices left much more residual variance. The distances, therefore, seem to exhibit qualities necessary for inferring the history of lineage splitting.

One of the lineages found in all trees unites *P. crinitus* with *P. eremicus* and *P. californicus*, corroborating Osgood's views on the makeup of *Haplomylomys*. Another lineage contains a *boylii-mexicanus* group joined by *P. (Podomys) floridanus*. A third lineage contains *P. leucopus*, and one-way comparisons suggest that *P. maniculatus* and *P. gossypinus* also belong to this clade. The three major lineages, *leucopus*, *Haplomylomys*, and *floridanus-boylii-mexicanus*, appear to have diverged at about the same time and the present data do not resolve the trichotomy. The median and modal stabilities support different placements. of *P. leucopus*, but on the bases of extremely short internodes. Of the outgroups, *Onychomys* was the closest to *Peromyscus*. This study suggests that DNA hybridization can contribute further to systematics of *Peromyscus* as well as other rodent groups. I expect that the anagenetic information produced by this technique, the branch lengths on the tree, will be a useful complement to cladistic information in the study of comparative biology and evolution, where *Peromyscus* serves as a model organism.

These studies are part of a Ph.D. program under the supervision of Dr. John A. W. Kirsch. Some of these species were represented by contributed tissue samples, for which I am extremely grateful.

* * *

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Benedict College maintains colonies of *Peromyscus maniculatus bairdii* and *P. polionotus*, derived from stocks at the University of South Carolina. Hybrids are produced from crosses of *maniculatus* females to *polionotus* males. There are two studies involving *Peromyscus* underway at present.

EFFECTS OF CHRONIC PCB EXPOSURE ON REPRODUCTION IN THE OLDFIELD MOUSE

Although production and distribution of PCBs was discontinued in the US by 1979, large quantities persist world wide. These lipophilic compounds are widely distributed through atmospheric transport and readily bioaccumulate. A number of biological effects have been noted such as increased incidence of cancer and diminished reproduction; however, there have been relatively few studies of sustained, low level exposure, as might be encountered in environmental contamination.

We are investigating the effects on reproduction of chronic (one year), low level PCB exposure with the old field mouse, *P. polionotus*. Monogamously mated pairs are being given 5 ppm PCB in the diet for 12 months while maintained under conditions of standard laboratory care with 18 hrs light: 6 hrs dark per day and various indicators of reproductive success monitored. Offspring of the exposed animals are maintained on the 5 ppm PCB diet and paried with offspring of other exposed pairs when adult. the investigation will continue through two generations of exposed animals. Upon the conclusion of the 12 month exposure of the pairs, body weights and organ weights will be recorded, along with assessment of activity and isozyme patterns of hepatic enzymes.

After 9 months summary results are as follows: % mated pairs with one or more litters--control 78, exposed 67; litters per pair per month--control 0.31, exposed 0.22; birth interval in days for first, second, third and fourth litters--control 74, 41, 45 and 41, exposed 58, 67, 60 and 110; young per litter at birth--control 3.7, exposed 3.5; young per litter at 25 days--control 2.2, exposed 2.0; birth weights--control 1.8 g, exposed 1.5 g; weight at 25 days--control 10.5 g, exposed 9.4 g. These findings suggest that even at this low level, chronic exposure to PCBs may affect reproduction.

INTESTINAL AND SERUM LEUCINE AMINOPEPTIDASE AND ALKALINE PHOSPHATASE OF *PEROMYSCUS*

Variation of intestinal and serum leucine aminopeptidase (LAP) and of alkaline phosphatase (AKP) was investigated by starch gel electrophoresis with *P. maniculatus*, *P. polionotus* and their F-1 hybrids. Within the two species, no individual variation was observed for serum intestinal LAP or AKP, although each species had a characteristic isozyme for each enzyme. The serum LAP of the hybrids resembled the isozyme of *maniculatus*, while the serum AKP of the hybrids was similar to that of *polionotus*. Neuraminidase digestion prior to electrophoresis affected all serum isozymes, indicating sialation of the protein.

Within each species intestinal LAP and AKP were similar when examined by starch gel electrophoresis and no variants were observed within the species. Intestinal AKP of the hybrids was like that of *polionotus*. All intestinal AKP isozymes were sensitive to neuraminidase. Three electromorphs of intestinal LAP were observed: one similar to the *polionotus* form, one similar to the *maniculatus* isozyme and a third which appeared to be a combination of the two. We are currently examining these enzymes in neonatal and juvenile animals.

* * *

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ALLONURSING IN *PEROMYSCUS MANICULATUS*

We are interested in various aspects of kin recognition in *Peromyscus maniculatus*. Our colony is derived from wild animals live-trapped from various locations in Chautauqua County, NY during 1982 and 1983. Our current work focuses on allonursing (communal nursing) in this species and the influences of kinship and prior maternal association on the process.

Communal *nesting*, wherein females combine litters and nurse simultaneously, is well-documented for *Peromyscus maniculatus*, but evidence for *allonursing* has been anecdotal and fragmentary. To conclusively demonstrate allonursing one must document actual exchange of pups between nursing females. We hypothesized that if genuine allonursing does occur in this species, it would be most evident in groups of closely related females and that the female's tendency, and possibly ability, to discriminate against another's pups would be minimized by a high degree of relatedness of the pups. Accordingly, sibling females were bred by the same male and caged together during gestation. As controls, unrelated females were bred by unrelated males and established as communal nest pairs upon birth of their litters. Daily records of female nursing for three weeks categorized female behavior as "parental nursing" if the female was nursing only her own pups; "nonparental nursing" if the female was nursing any combination of pups which included at least one non-offspring; or "not nursing" if the female was not nursing any pups at the time. Analysis of our data to date suggest the following conclusions:

(1) Allonursing is a prominent feature of maternal behavior in this species. Females readily exchange pups with both sibling and unrelated cage-mates.

(2) The tendency to allonursing appears to be enhanced by kinship and prior association. Or alternatively, the female's ability to discriminate against another's pups may be reduced by a high degree of genetic relatedness of the pups.

(3) Pairs of allonursing, sibling females spend significantly more time engaged in non-nursing activities. It is likely that allonursing, in addition to enhancing "inclusive fitness" through increased nursing efficiency and the energetic (thermal) advantages of "huddling", may also enhance fitness by allowing more non-nursing behaviors (e.g., foraging, exploration, predator deterrence, etc.).

* * *

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* **CALL FOR COLLABORATORS:** *
* **Field-trapped *Peromyscus* which** *
* **present with anemia or an** *
* **immunodeficiency-like disease.** *
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SEARCH FOR NOVEL LENTIVIRUSES IN WILD MICE

We are studying novel lentiviruses in many animal species. These viruses, which include HIV (human immunodeficiency virus), are a subset of retrovirus which are associated with chronic infections and immunodeficiency. Lentiviruses have been demonstrated in animals ranging from man to cats. Recent evidence regarding FIV (feline immunodeficency virus) indicates that between 1-2% of all pet cats in the U.S. are infected. In addition, stray cats or domesticated cats which roam wild are >40-fold more likely to be infected with FIV. Although several cases have been described in which it seems that cats were infected by fighting with stray cats, this scenario is insufficient to explain the large percentage of FIV-positive cats, most of which are totally house-bound. Thus, we have postulated that roaming cats may become infected via interaction with wild mice.

We have developed a set of degenerate DNA primers for PCR (polymerase chain reaction) which can identify *pol* sequences from any of the known lentiviruses. In order to increase the chances of isolating a novel murine lentivirus, we are most interested in finding *Peromyscus* strains trapped in the wild which exhibit characteristics of an immunodeficiency: weakness, anemia, chronic respiratory and ocular infections. In the absence of such a phenotype, we believe, based on the cat results, that we would have to trap and test several hundred "normal" wild-mice to possibly find such an agent. Thus, we are appealing through this newsletter to researchers who either may have caught such animals (and, if lucky, may still have the animal or some frozen blood) or know of a region where such mice are typical. My desire is to establish collaborative studies along these lines.

* * *

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Ron M. Adkins and Rodney L. Honeycutt have been conducting research on the molecular systematics and evolution of divergent rodent lineages. This research has involved comparative studies of nucleotide sequence variation in the mitochondrial cytochrome c oxidase II gene (COII). Some of the taxa examined thus far include *Peromyscus*, *Onychomys*, and several other peromyscine and sigmodontine rodents as well as more divergent rodent lineages. In addition to this research, Laura Janecek and Rodney Honeycutt have been investigating the rodent insulin gene duplication, and the preliminary results suggest that *Peromyscus* and related forms have one insulin gene with two introns, the more common arrangement seen in mammals and non-murine rodents.

* * *

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My study of the behavior of *Peromyscus* has been ongoing for nearly five years. It started when I observed similarities in behavior patterns of these mice and in the people that I had been interviewing for material for a book I am writing. This study includes the use of photographs to document my observations and findings whenever possible. The focus on behavior includes population control, aggressiveness, intelligence, cleanliness - or lack of it - from one family to another, reaction differences between the sexes, relationships of family groups, and comparing behavior of one family with that of a another family.

Working closely with these tiny animals has allowed me to observe and record happenings that seem almost unbelievable, including examples of affection, grief, and cooperation to help a distressed individual. I have observed parental care by both parents, even to the carrying of pups that had strayed from the nest, back to it when the male was not the parent. (The female was already pregnant when she was placed in the male's cage.) I have watched a surrogate mother raise three orphaned pups along with her own two. (The orphans, three days older than her pups, were placed with her when five days old.) I successfully handraised four pups orphaned before their eyes were open, and later one pup from another litter that had been orphaned.

My colony of mice have produced a large variation of coats, with unusual markings and colors. One mouse has a very crooked nose. Another was born with three legs. In spite of this she learned to flip to the cage top and walk upside down by hanging to the hardware cloth top. There are mice with kinked tails, unusually long tails, and some tails used to aid in balance when the mice climb. Faces and markings differ in many individuals. I have one male that survived after his mother ate off most of one of his hind legs. (His siblings did not fare so well.) I have had bald or near-bald pups. In fact I have six at the present time.

I have mice that are acrobats, mice that are shy, while others "show off." They play, fight, cuddle, groom each other as well as themselves, hoard food, thump feet; one even slides through between her water bottle and the holder after her backward flips to the cage top. Each one is individual. I have learned that there can be few generalities made about traits or behavior happening because of species. As soon as I am quite certain that I have discovered a trait attributable to this species, an individual does something to refute my theory.

I have just read PN #6 and wonder if my near-hairless mice are one of the mutant types written about in that issue. I have had pups with bald spots before, but only four with such widespread baldness and none of them lived very long. The ones with smaller blad spots soon grew hair and appeared normal. Occasionally I have had adults with bare backs and/or hips, but I had attributed that to nest building and/or fighting.

The near-hairless pups that I have now have their eyes open, are eating at the food dish, drinking from the water bottle, and are running on the exercise wheel, but still nurse on more than one female. This afternoon two different females have dragged pups hanging onto their nipples, out of the nursery jar. One pup was even dragged onto the exercise wheel and was given a bumpy ride until it finally fell off. The pup ran back to the jar and a female went in after it. She licked and nuzzled it until the pup finally got up and began licking her on the face and ear.

I shall watch the progress of these little ones, anxious to see if they will grow a normal coat as some of the others did, or if they will remain near-hairless as they are now. They are active and appear in good health, while one near-hairless one that I had about two years ago always appeared fragile and strange. The other three that I had about two and a half years ago started out all right, but as the lost more and more hair, they seemed to lose vitality and just died, one-by-one. (I have photographs of two or three of them.)

KLEIN (Continued):

Of the near-bald pups that I have now, some are nearer nude than others. Some still have patches of hair on their backs, but some only have hair on their bellies. Their parents are part of a family that have produced greyish coats, near white coats, very reddish coats, and coats with white spots and streaks on sides and backs of some individuals. One of the females nursing this group had white spots on her side when she was younger. The spots seemed to disappear for a while, but are back now. One of the other females nursing has a very red coat (light red, not mahogany-colored). She probably is the daughter of the spotted one. The male is one of the spotted one's sons. He was the only male in the tank at that time so had to be the male parent of all of the near-bald pups. The largest of the pups seems to stay close to the spotted female. Often they go to a separate jar from the others. It is not quite as bald as the smaller ones. I suspect it may be a couple of days older and and belong to this spotted doe, while the others may belong to one of the other females that are in the jar with them.

The possiblilty that I may have mutants in this colony of *Peromyscus* adds a new interesting dimension to my study. It must now go beyond a behavioral study, especially if these pups live to reproduce.

I would like to hear from any of you who have seen this type of mutant, and would be willing to send me your thoughts about my pups.

I will report on the pups' progress, and survival rate in future issues of PN.

* * *

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DO PEROMYSCUS PREY ON BIRD EGGS?

Small rodents long have been suspected to be predators of the eggs of ground-nesting birds (Wynne-Edwards 1952; Criddle *in* Bent 1968; Parmelee *in* Bent 1968; Custer and Pitelka 1977). In a study on a spotted sandpiper population in Minnesota, Maxson and Oring (1978) found reduced clutch sizes due to overnight damage of eggs. Trapping of *Peromyscus* and *Microtus* reduced the rate of damaged eggs. None of 11 clutches that were laid after the small mammal trapping were lost. This study is the only report of loss of eggs due to *Peromyscus*. We documented predation on artificial ground nests by white-footed mice (*Peromyscus leucopus*) in forest interior habitats not by indirect cues of predator removal, but by pictures that were obtained when the mice approached the nests.

The study was designed to determine factors that increase predation pressure on nests of ground nesting birds in forest interior habitats. A total of 240 artificial nests were laid out from May to July. For one week every month 10 nests were placed on eight sites (4 ha) within forests of the Shenandoah National Park and the National Zoo's Conservation and Research Center in Virginia. In June and July 8 of the ten nests on each study site were monitored with an automatic camera to identify the nest predators. In August each study site was live-trapped for small mammals for 72 hours to determine whether predation rates were correlated with population densities of small mammals.

LEIMGRUBER and McSHEA (Continued):

The total number of robbed nests was 69 (29%). 14 of these 69 nests were without camera and no predator could be identified. The predator could be identified in 48 of the 55 robbed nests that were monitored by a camera system (87%). In many cases more then one predator species appeared subsequently at the nest site. Therefore 128 pictures of 76 different predators were taken at 48 nests. 14 different predator species were identified and 18 of the 128 pictures showed white-footed mice. White-footed mice appeared at 9 different nest sites and were presumably responsible for 11.8% of the nest losses. Together with black bears (*Ursus americanus*) (9 pic.), white-footed mice were the third most common predator after striped skunks (*Mephitis mephitis*) and eastern gray squirrels (*Sciurus carolinesis*).

The number of white-footed mice pictures taken at each study site was not significantly correlated (Spearman-rank for $n=8$; $r = 0.4108$; $P = 0.1$) with the number of white-footed mice that were trapped.

In continuous forests of the Shenandoah National Park white-footed mice are important nest predators on ground nests and they might exacerbate the plight of already threatened migratory birds such as Kentucky warblers (*Wilsonia critinia*), worm-eating warblers (*Halmitheros vermivorus*) and ovenbirds (*Seiurus aurocapillus*). That density was not significantly correlated with number of pictures taken might be due to the small sample size. However, this study shows that white-footed mice are at least as important nest predators on birds' nests as raccoons (*Procyon lotor*) (10 pic.).

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IN SITU GENE MAPPING OF *PEROMYSCUS MANICULATUS BAIRDII*

This past June we began a project that will involve assigning selected genes to chromosomes in the deer mouse. This effort is coordinated with the work of Dr. Dawson's group who are primarily concerned with expanding the *Peromyscus maniculatus bairdii* linkage map. We are using short-term spleen cultures supplemented with growth factors to obtain cell lines with high mitotic indices. We will first produce a Q-band karyotype that we can relate to the new G-band standard karyotype. In this manner, each chromosome will be unambiguously identified via Q-bands. The in situ effort will involve staining chromosomes with fluorochromes to produce both Q-bands and biotin labelling. Thus, the same metaphase spread can be photographed using different UV wavelengths to document the position of a gene on a chromosome and to identify the chromosome pair on which the gene resides. Initially, we will attempt to map multiple-copy genes using either *Mus* or human probes. As this technology advances, we will begin mapping single copy genes.

* * *

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Taxonomy of Midwest *Peromyscus leucopus* and *P. maniculatus*

We, and other midwest researchers, have had difficulty in unequivocally identifying *Peromyscus leucopus noveboracenis* and *P. maniculatus bairdii* in field situations across different habitats and during different seasons. Captured mice did not always follow the dichotomy reported by Bowles (Spec. Pub. Mus. Texas Tech Univ., 9, 1975) for tail length and hind-foot length. We wanted to examine, locally, external and cranial measurements or *Peromyscus* to attempt to better define external characteristics for field identification. We obtained specimens from around Cedar Falls, Iowa, prepared by a field zoology class under the supervision of OAS. Specimens were initially identified by attempting to use Bowles; criteria, and sexes were separated. We took the standard external measurements and the 11 cranial measurements described by Choate (J. Mamm. 54:41-49, 1973) to analyze using a stepwise discriminant function (BMDP7M). We ran the analysis and reclassified three specimens based on the posterior probability of group membership. A second analysis then correctly classified all specimens using the following significant measurements in forward stepwise order: zygomatic breadth, tail length, and pterygoid breadth. The means (±SD) of these measurements in millimeters were:

	P. leucopus		*P. maniculatus*	
	male	female	male	female
Zygomatic breadth	13.78±0.217	13.65±0.182	14.45	12.97±0.336
Tail length	70.80±2.860	60.50±4.796	65.00	54.66±8.501
Pterygoid breadth	1.59±0.172	1.59±0.213	2.20	1.75±0.360
Sample size	10	4	1	3

We did not conclude that pelage characteristics were useful in separation of species. The above overlap of tail length illustrates the problem with external quantitative characteristics. Hence, our attempt to answer this question was not successful. We hope to expand this study. We were not able to analyze amylase enzymes from these specimens. Details of the analysis and specimens are available from OAS.

* * *

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In a recent series of papers, Haigh presented evidence that less than 3% of young female white-footed mice (*Peromyscus leucopus noveboracensis*) reproduce by 300 days of age if, in addition to the male, an adult female is present. Removal of the adult female after 150 days was followed by reproduction by the previously inhibited younger female. Subsequent work showed that first estrus occurred at an average of 40 days of age in young females housed with an adult male and female and that ovulation and insemination were normal. Implantation of fertilized eggs (blastocysts) in the uterus, however, was disrupted. Simultaneous experiments showed that young females exposed (without physical contact) to bedding soiled by adult females or to the urine of adult females were likewise reproductively inhibited. Thus the evidence indicated that an air borne chemical, present in the urine of adult females, functioned to prevent implantation of blastocysts in the uteri of younger females.

During the past two years we have explored this phenomenon in the offspring of adults of this subspecies recently captured near Williamsburg, Virginia. These experiments (in press, J. Mamm.) have demonstrated: (1) that 69% of young females reared from weaning (21 days of age) in the presence of an adult bisexual pair (parents or not) reproduced by 150 days of age; and (2) that being with an adult female from 21-90 days of age stimulated reproduction by these young females compared to being reared in isolation.. Our data show a markedly higher rate of reproduction among Virginia mice than Haigh reported for Michigan mice of the same subspecies maintained similarly, and are thus in direct contradiction to those of Haigh.

Recently, with the help of John A. King at Michigan State University, we have collected white-footed mice from the same general area where Haigh's mice came from and are repeating these experiments with both Virginia and Michigan mice under the same conditions in our laboratory. This research focuses on the following questions:

(1) Is the phenomenon of adult female induced reproductive suppression of young females, as demonstrated by Haigh, a generalized phenomenon?

(2) Do Virginia mice and Michigan mice of the same subspecies studied by Haigh respond differently when both are tested in the same laboratory under identical conditions?

(3) Is there evidence that the reproductive response of young females to the presence of adult females varies across the geographical range of the same subspecies?
These experiments will be completed in early 1992.

In press: A study of reproductive inhibition in female white-footed mice from Virginia. (J. Mamm.)

* * *

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Potassium Evoked In Vitro Release of (3H)-Acetylcholine from the Frontal Cortex of Boggler, Juvenile Ataxia, and Wild-Type *Peromyscus*.

The primary interest of the Neurological and Behavioral Mutant Center, as part of the *Peromyscus* Stock Center, is to characterize new and naturally occurring oligogenic behavioral mutants both genetically and behaviorally, and to find neuroanatomical and neurochemical correlates of these disorders, particularly where they mimic similar disorders in man. To this end, the level of potassium-evoked release of (3H)-Acetylcholine has been compared in two different mutant stocks and a wild-type control stock maintained at the center. Six non-sibling representatives of each of the following three stocks were compared.

Boggler (bg)--This mutant stock was isolated from descendents of *P. maniculatus blandus* trapped near Tularosa, NM in 1947. This mutant has subsequently been crossed many times in sucessive generations to our standard *P. maniculatus bairdi* BW stock. Boggler homozygotes show an early aging behaviorally, and have a pronounced tremor both at rest and during movement, with an ataxic gait. Neuroanatomically, age and sex-matched homozygotes have a statistically significant greater number of dystrophic axons at all ages than do wild-type homozygotes.

Juvenile Ataxia (ja)--Juvenile ataxia was isolated from a stock of *P. maniculatus bairdi* wild-trapped near East Lansing, Michigan in 1975. Homozygotes under 35 days of age display a severe ataxia with hypertonus, falling to either side with equal frequency. Between 35 and 45 days of age, homozygotes show a rapid improvement, with nearly complete recovery from behavioral deficits.

Wild-type stock--The control stock, used for outcrossing mutant stocks and which serves as a control for all experimental procedures is a stock of wild-type *P. maniculatus bairdi* designated BW. The BW stock is descended from less than 20 animals originally trapped between 1942 and 1943 in Washtenaw County, MI. This stock has since been maintained as a closed colony, with no additional animals contributing to the gene pool.

Comparisons between the total potassium-evoked increase in release of (3-H)-Acetylcholine from the frontal cortex of six animals of each of the above three stocks using essentially the in vitro method of Hadhazy, showed no significant differences between the wild-type BW stock (mean+320.3 $\pm$ 16.4) and boggler homozygotes (mean=313.3 $\pm$ 16.4).

Comparisons between wild-type and juvenile ataxia homozygotes (mean=232.7 $\pm$ 20.8), showed approximately a 27% decrease. The reason for this difference, and its potential effect on neuronal development and aging is not yet clear, but is currently under investigation. Since, however, cholinergic neurons have been shown to play a key role in cognitive and motor functions, these findings are very intriguing.

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Molecular Studies of Alcohol Dehydrogenase Genes in Deermouse

Previous work has established an ADH-negative strain of *Peromyscus maniculatus* which is deficient for expression of alcohol dehydrogenase activity due to the Adh^{N} allele. Homozygous animals for this allele lack enzyme activity and immunocrossreacting material is not found in these mice using monospecific antibody to the active enzyme.

A mouse Adh-1 cDNA clone was used to isolate several cross-hybridizing clones from deermouse liver cDNA libraries. Two classes of clones were isolated from ADH-positive deermouse cDNA library and only one from an ADH-negative cDNA library. From sequencing data these two classes of cDNA clones are shown to represent two different Adh genes. One, which is present only in ADH-positive deermice, has 92% homology to mouse Adh-1 gene and is the Adh-1 gene (Class I) in deermouse. Another cDNA has only 65% homology to mouse Adh-1 cDNA. This cDNA also has less than 65% homology to Class II and Class III human ADHs and may represent a new class. Both these genes are expressed mainly in liver and kidney.

Southern analysis indicates that most if not all of the Adh-1 gene in ADH-negative deermice is deleted, which explains the lack of ADH activity and lack of immunocrossreactivity.

The cDNAs present in both ADH-positive and ADH-negative deermice (Adh-2 gene) share 99% homology and encode a protein with highly conserved and important structural domains shown by all 18 examined ADHs, including ADHs from plants and yeast. Therefore, this cDNA may represent a functional Adh gene and code for a new enzyme class.

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