PEROMYSCUS NEWSLETTER

Number Forty-One

Fall 2006

Cover: A wild *Peromyscus* with the tan streak color pattern found in Alberta, Canada. We believe the species to be *Peromyscus maniculatus borealis*. The tan streak animals in the PGSC colony originated from a closed colony of *P. maniculatus nubiterrae* trapped in the southern Blue Ridge Mountains of Macon County, North Carolina. This mouse, however, was trapped at 56-38-30 N by 123-23-24 W, elevation 1,111 meters.

Photograph by Frank Ritcey, Operations Manager, Christina Falls Outfitters

***Peromyscus Newsletter* Number 41**

This is the second exclusively electronic issue of *PN* and the second for which I have been editor. I would like to thank all of you who have been so supportive with your well-wishes and comments for improving the newsletter. The feedback has been very helpful, so keep it coming! Just send me an email at peromyscusnewsletter@biol.sc.edu.

One difficulty I have encountered for which I have no solution is the frequency of returned emails when I send notices to the list. I believe many if not most are legitimate addresses but the recipient's server will not allow the message to pass due to the long list of undisclosed recipients. I will try to contact as many of these people as possible about the problem, but if any of you know someone who has not been getting their emails I would be grateful if you could ask them to check their spam filters and send me an email so I may verify their correct email address.

As the size of the electronic *PN* poses a problem for many people's servers, I will no longer send it as an attachment. Instead, you may view and download the latest version at http://stkctr.biol.sc.edu/ and click on the Newsletter tab. Several people mentioned they print out the *Newsletter* instead of reading it on their computers. The switch to a plain white background is an attempt to increase readability under those circumstances.

Finally, and most importantly, we say goodbye to the Stock Center director for the past 6 years, Dr. Mike Dewey, who retired at the end of August. He is replaced by Dr. Mike Felder (director) and Dr. Gabor Szalai (associate director). More information about our new directors and a farewell tribute to Dr. Dewey are included in this issue. I hope you enjoy.

Julie

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News, Comments, and Announcements:

Published in *Molecular Phylogenetics and Evolution* 40 (2006): 251-258 is a paper by S. A. Reeder et al entitled "Neotomine-peromyscine rodent systematics based on combined analyses of nuclear and mitochondrial DNA sequences". These authors recommended the following genera should be included in the Peromyscini: *Habromys*, *Isthmomys*, *Megadontomys*, *Neotomodon*, *Onychomys*, *Peromyscus*, *Podomys*, and *Reithrodontomys*.

♦♦

The 2006 annual meeting of the American Society of Mammalogists took place Saturday June 17 to Wednesday June 21, 2006 at the University of Massachusetts, Amherst. There were 7 presentations relating to *Peromyscus* research, some of which are included in the contributions section. Presentations not in the contributions section are summarized below.

♦♦

Presented at ASM 2006 was THE EFFECTS OF BOT FLY PARASITISM ON MOVEMENTS OF *PEROMYSCUS LEUCOPUS* by Michael J. Cramer & Guy N. Cameron of the University of Cincinnati. They reported that although there was no overall effect of infection on distance moved, females tended to move less when infected than males, and there was no difference in movement between individuals with a single infection and those harboring several larvae.

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Also at ASM 2006 was POPULATION GENETICS OF THE DEER MICE, *PEROMYSCUS MANICULATUS*, FROM THE WARNER MOUNTAINS OF CALIFORNIA: ONE LINEAGE OR TWO? by Stephanie A. White, Stephanie MacDonald, Allison Ivancovich, Leslee A. Parr & John O. Matson. By sequencing the mitochondrial D-loop they confirmed the results of an earlier study demonstrating there are two distinct maternal lineages in this single population residing in the Warner Mountains.

♦♦

At ASM 2006 a poster was presented entitled COAT COLORS OF MALE AND FEMALE *PEROMYSCUS MANICULATUS*: UNEXPECTED DIFFERENCES by Laurie Gayes & Virginia Hayssen of Smith College, MA. Using a chromometer to measure 3 color components, these authors not only found that agouti coats had higher values, they found an unexpected sex difference not distinguishable to the human eye. For both coat colors, males displayed higher values than females.

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Also at ASM 2006 was work done at the PGSC, *PEROMYSCUS* GENETIC LINKAGE COMPARISONS WITH *RATTUS* AND *MUS* by Julie L. Weston, Clifton M. Ramsdell, Adrienne Lewandowski, Travis C. Glenn & Michael J. Dewey. This was based on Cliff Ramsdell's PhD work demonstrating that *Peromyscus* genome arrangement is more similar to *Rattus* than *Mus*. Look for Cliff's results in future issues of *PN* and other refereed journals.

♦♦

Recently published was the third edition of **Mammal Species of the World** edited by Don E. Wilson and DeeAnn M. Reeder. It is a 2-volume set available through The Johns Hopkins University Press, 2715 N. Charles Street, Baltimore, MD 21218 Phone: 1-800-537-5487 Web Address: www.press.jhu.edu

♦♦

Contribuciones Mastozoológicas en Homenaje a Bernardo Villa has just been published by Victor Sánchez-Cordero and Rodrigo Medellín, editors. Chapter 13, "Peromyscine Biogeography, Mexican Topography and Pleistocene Climatology" is written by our own Wally Dawson. Although we do not have a copy of the book itself, we have reprints of Dr. Dawson's chapter, and anyone wishing to receive a copy should email: peromyscus@stkctr.biol.sc.edu

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According to the Centers for Disease Control and Prevention, there may be a greater risk for human hantavirus infection this year. During January-March 2006, a total of nine confirmed cases of Hantavirus Pulmonary Syndrome were reported from Arizona, New Mexico, North Dakota, Texas, and Washington. Six of the nine cases were in Arizona and New Mexico (we reported on 2 from Arizona in the last issue, PN40). The elevated risk is believed to be the result of increased rainfall in the past 2 years leading to increased vegetative biomass, higher rodent populations, and increased virus transmission.

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Recently published in March 2006 is "The Geography of Mammalian Speciation: Mixed Signals from Phylogenetics and Range Maps" by Benjamin M. Fitzpatrick and Michael Turelli (Evolution 60(3): pp. 601-615). These authors reported evidence that allopatric, not sympatric, speciation was responsible for the diversity of species in the *Peromyscus boylii* group.

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Help out a researcher in need! Justin Boyles at the Department of Ecology and Evolution, Indiana State University is studying latitudinal variation in pelage insulation in *Peromyscus leucopus* and *P. maniculatus* across their ranges. He needs 8-10 adults of both species trapped in winter (Dec-Feb) from as many sites as possible. If you can help him out contact him for shipping and handling instructions at jboyles3@indstate.edu

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Looking for a *Peromyscus* project for yourself or a student? The Stock Center has recently been contacted about the availability of a wonderful resource. Dr. Wendel Johnson of the University of Wisconsin – Marinette has ecological, morphological, and reproductive data for over 1000 snap-trapped and live-trapped *Peromyscus maniculatus maniculatus* from Isle Royale National Park. They were collected from 1966-68 while working on his PhD at Purdue University under the direction of Dr. Durward Allen. According to Dr. Johnson, little has been published from this data set and he is readying the collection for deposition in the Field Museum in Chicago. Anyone interested should contact him directly at wjohnson@uwc.edu or through us at peromyscusnewsletter@biol.sc.edu.

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Congratulations to Dr. Clifton Ramsdell, the PGSC's newest PhD! On September 20, 2006, Cliff successfully defended his dissertation entitled, "Comparative Genome Mapping of the Deer Mouse (*Peromyscus maniculatus*)". He was Dr. Mike Dewey's final graduate student at the University of South Carolina and made us all proud!

♦♦

Congratulations to our Associate Director, Dr. Gabor Szalai, and his wife, Dr. Monika Veres, on the birth of their daughter, Boglárka Eszter Szalai, born October 16, 2006.

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Several *Peromyscus* researchers have begun discussing the benefits of a full genome sequence for the genus. We are actively soliciting input from the research community and if the response is positive we will send a separate email to the list to coordinate the writing of a white paper for the project. Send comments to: peromyscusnewsletter@biol.sc.edu

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Collaborators Wanted in Studying Genetics of Reproductive Isolation in the *Peromyscus maniculatus* Species Complex

We have been studying reproductive isolation in the *Peromyscus maniculatus* species complex. It has long been known that there existed variation in producing *P. maniculatus – P. polionotus* hybrids, and that other populations within this species complex display variable degrees of success in inter-population matings (Dice, 1949; Liu, 1953; Liu, 1954; Watson, 1942). Wally Dawson first showed that the *P. maniculatus – P. polionotus* hybrids showed parent-of-origin effects on growth and development (Dawson, 1965). With colleagues, he did numerous further studies including ruling out mitochondrial DNA – nuclear DNA incompatibilities as the cause of the hybrid dysgenesis (Dawson, 1982; Dawson et al., 1993; Rogers and Dawson, 1970). As an alternative hypothesis, the authors speculated that incompatibilities in regions of the genome harboring imprinted genes might be responsible (Dawson et al., 1993). Imprinted genes are expressed from only one parental allele and are known regulators of growth and regulation. DNA methylation, a common epigenetic modification, appears to be a primary regulatory mechanism of this phenomenon (Vrana, 2006), and has been shown to be perturbed in other mammalian interspecific hybrids (O'Neill et al., 1998).

Our work has shown that imprinted gene expression and DNA methylation are perturbed in the hybrids (Duselis et al., 2005; Vrana et al., 1998; Vrana et al., 2001). Genetic analysis to date has shown that both imprinted domains of the genome and a maternal effect locus are involved in the hybrid dysgenesis (Duselis et al., 2005; Loschiavo et al., 2006; Vrana et al., 2000). We propose that the same or similar loci and similar epigenetic changes are involved in isolating other populations within this species complex. Little work has been done on population genetics of genomic imprinting or epigenetics in any species. This work will have implications for human disease as well as reproductive isolation.

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THE *PEROMYSCUS* GENETIC STOCK CENTER

General

The University of South Carolina has maintained a genetic stock center for *Peromyscus* (deer mice and congeneric species) since 1985. The center was established under a grant from the Living Stocks Collection Program of the National Science Foundation and continues to be supported by NSF and the NIH Biological Models and Materials Research Program. It also receives support from the University and from user fees.

The major function of the Stock Center is to provide genetically characterized types of *Peromyscus* to scientific investigators and educators. Continuation of the center is dependent upon significant external utilization, therefore potential **users are encouraged to take advantage of this resource**.

Policies and Procedures

The Stock Center maintains several categories of stocks of living animals: 1) Closed colony random-bred[1] "wild-type" stocks of seven species of *Peromyscus*. 2) Two highly inbred[2] stocks of "wild-type" *P. leucopus*. 3) Stocks of fifeen coat color mutations, mostly in *P. maniculatus*. 4) Stocks of eight other monogenic traits. The Stock Center operates in strict compliance with the Animal Welfare Act and is located in an AAALAC approved facility. All animal care is performed by certified technicians. Stocks are monitored regularly for presence of disease and parasites and are free of hantavirus and 15 murine viruses.

The Stock Center also provides blood, organs, tissues, fetuses, skins and other biological materials from *Peromyscus.* The Stock Center operates a Molecular Bank where selected genomic libraries and probes are available. Other resources include a reference collection of more than 2,500 reprints of articles on peromyscine rodents, copies of which may be provided. The Stock Center is the primary sponsor of ***Pero*Base**, an on-line database dedicated to information regarding *Peromyscus* and closely related species.

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. Animals requested in greater numbers frequently require a "breed-up" charge and some delay in shipment.

Orders and Pricing

A user fee is charged for animals or materials provided by the Stock Center. A schedule of fees is shown on the next page. Fees vary with species and type of service provided. User assumes the cost of all shipment. Animals lost in transit are replaced without charge. Tissues, blood, skins, *etc*. are supplied at a modest fee that includes technician time. Arrangements for special orders will be negotiated. Billing will be submitted upon satisfactory delivery. **Write or call for details or special requirements.**

SCHEDULE OF USER FEES

Item	Academic and Government	Commercial
MATURE ANIMALS (each)		
Wild-type Stocks		
Smaller species (*P. maniculatus, P. polionotus, P. leucopus, P. eremicus*)	**$ 22.50**	**$35.00**
Larger species (*P. californicus, P. melanophrys, P. aztecus*)	**30.00**	**40.00**
Mutant and Inbred Stocks	**30.00**	**40.00**
Pregnant females (Smaller species)	**40.00**	**50.00**
(Larger species)	**55.00**	**65.00**
Special Attention (Diet, *etc*.)	**40.00**	**50.00**
F_1 Species Hybrids	**30.00**	**40.00**
TISSUE SAMPLES (Per sample)		
Solid	**25.00**	
Fluid (Blood, urine, saliva, etc.) per ml	**40.00**	
Flat skins (each)	**35.00**	
MOLECULAR MATERIALS		
Extracted DNA, 20 µg	**100.00**	
PCR Primers (500 µl @ 10 µM)	**10.00**	
Genomic & cDNA libraries	**300.00**	

OTHER CHARGES

Shipping costs = actual shipper's charges plus cost of mouse containers, packaging.

Lab fee for sample preparation.

Breed-up fees (for orders exceeding 50 animals) = *per diem* cage charges X cages required.

STOCKS AVAILABLE

WILD TYPE STOCKS	**ORIGIN**
P. maniculatus bairdii (BW Stock) Deer Mouse	Closed colony bred in captivity since 1948. Descended from 40 ancestors wild-caught near Ann Arbor MI.
P. maniculatus sonoriensis (SM2 Stock) Sonoran Deer Mouse	Derived from about 50 animals wild-caught by Jack Hayes in 1995 near White Mountain Research Station CA.
P. polionotus subgriseus (PO Stock) Oldfield Mouse	Closed colony since 1952. Derived from 21 ancestors wild-caught in Ocala Nat'l. Forest FL. High inbreeding coefficient.
P. polionotus leucocephalus (LS Stock) Beach Mouse	Derived from beach mice wild-caught on Santa Rosa Island FL between 1987-1988 and bred by R. Lacy.
P. leucopus (LL Stock) White-footed Mouse	Derived from 38 wild ancestors captured between 1982 and 1985 near Linville NC.
P. californicus insignis (IS Stock) California Mouse	Derived from about 60 ancestors collected between 1979 and 1987 in Santa Monica Mts. CA.
P. aztecus (AM Stock) Aztec Mouse	Derived from animals collected on Sierra Chincua Michoacan, Mexico in 1986.
P. melanophrys (XZ Stock) Plateau Mouse	Derived from animals collected between 1970 and 1978 from Zacatecas, Mexico and bred by R. Hill.
P. eremicus (EP Stock) Cactus Mouse	Originated from 10-12 animals collected at Tucson AZ in 1993.

INTERSPECIFIC HYBRIDS	
P. maniculatus X P. polionotus F_1 Hybrids	Bred by special order.
P. leucopus X P. gossypinus F_1 Hybrids	Sometimes available by special arrangement.

[3]**COAT COLORS**	**ORGINAL SOURCE**
Blonde *bln/bln*	Mich. State U. colony (Pratt and Robbins, 1982)
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)
[4]Brown *b/b*	Huestis stocks (Huestis and Barto, 1934)
California blonde *cfb/cfb*	Santa Cruz I., Calif., stock (Roth and Dawson, 1996)
Dominant spotting *S/+*	Wild caught in Illinois (Feldman, 1936)
Golden nugget b^{gn}/b^{gn}	Wild caught *P. leucopus* (Horner and Dawson, 1993)
Ivory *i/i*	Wild caught in Oregon (Huestis, 1938)
Platinum *plt/plt*	Barto stock at U. Mich. (Dodson et al., 1987)
[4]Silver *sil/sil*	Huestis stock (Huestis and Barto, 1934)
Tan streak *tns/tns*	Clemson U. stock from NC (Wang et al., 1993)
Variable white *Vw/+*	Mich. State U. colony (Cowling et al., 1994)
White-belly non-agouti a^w/a^w	Egoscue's "non-agouti" (Egoscue, 1971)
Wide-band agouti A^{Nb}/a	Natural polymorphism U. Mich. (McIntosh, 1954)

OTHER MUTATIONS AND VARIANTS

Alcohol dehydrogenase negative	Adh^0/Adh^0	South Carolina BW stock (Felder, 1975)
Alcohol dehydrogenase positive	Adh^f/Adh^f	South Carolina BW stock (Felder, 1975)
Boggler *bgl/bgl*		Blair's *P. m. blandus* stock (Barto, 1955)
Cataract-webbed *cwb/cwb*		From Huestis stocks (Anderson and Burns, 1979)
Epilepsy *epl/epl*		U. Michigan *P. m. artemisiae* stock (Dice, 1935)
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 (Van Ooteghem, 1983)
Enzyme variants		Wild type stocks provide a reservoir of variants (Dawson, 1983)

[1] "Random bred" without deliberate selection, sib-sib matings avoided. [2] Inbred lines bred by sib-sib and/or parent-offspring mating for 21 generations or more. [3]Unless otherwise noted, mutations are in *P. maniculatus*.
[4]Available only as silver/brown double recessive.

Other Resources of the *Peromyscus* Stock Center

Highly inbred *P. leucopus* (I_{30+}) are available as live animals or as frozen tissues. Two lines developed by George Smith (UCLA) are currently maintained by the Stock Center.

Limited numbers of other stocks are on hand, but not currently available. Inquire.

Preserved or frozen specimens of types given in the above tables.

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

Reference library of more than 2500 reprints of research papers, articles and reports on *Peromyscus.* Single copies of individual articles can be photocopied and mailed. Please limit requests to not more than five articles at any given time. There will be a charge of 10 cents per photocopied page after the initial 20 pages.

Photocopies of back issues of *Peromyscus Newsletter* ($5 ea.) or single original back copies, when still available, without charge.

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

For additional information or details about any of these mutants, stocks or other materials contact: Janet Crossland, Colony Manager,* Peromyscus *Stock Center, (803) 777-3107, e-mail crosslan@biol.sc.edu

PLEASE CALL WITH INQUIRIES

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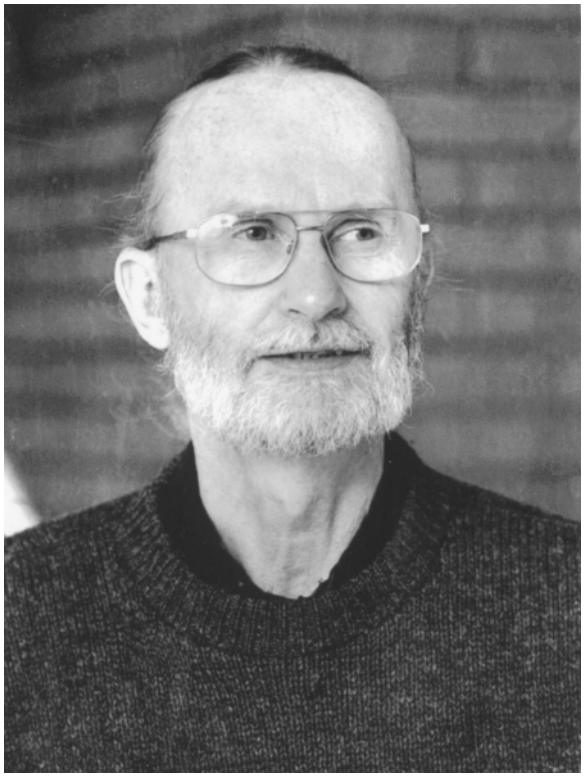
Farewell and Good Luck to Dr. Michael J. Dewey

The *Peromyscus* Genetic Stock Center is sad to say farewell to our director for the past 6 years, Dr. Michael J. Dewey. For those of you who know him, and for those of you who do not, we offer this insight into the man who has spent the last several years advancing *Peromyscus* research.

Mike grew up in Rawlins, Wyoming with a full-time mother and a father who worked on the railroad. It is no wonder, then, that Mike grew to love trains, travel, and the great outdoors. After graduating high school, Mike decided to enroll at the University of Wyoming where he earned his B.S. in microbiology. After that, his outgoing personality and love of foreign countries led him to join the Peace Corps, where he taught biology and biochemistry at the University of San Carlos in Guatemala City from 1966-68. Still fascinated with microbiology, Mike was accepted into the graduate school of the University of Pennsylvania, Philadelphia. After spending several years studying DNA metabolism and processing in T4 phage-infected *Escherichia coli*, Mike completed his PhD in 1973. After graduation he decided to pursue a postdoctoral position, so he continued at the University of Pennsylvania for another 5 years working with Dr. Beatrice Mintz producing mutant mice from embryonic stem cells at the Institute for Cancer Research in Philadelphia.



In 1979, Mike accepted a faculty position in the Department of Biological Sciences at the University of South Carolina. Since then, Mike has been an excellent mentor to 6 postdoctoral researchers, 6 PhD students, 6 MS students, and undergraduates too numerous to count. He is an outstanding teacher instructing courses in cell and molecular biology, developmental genetics, developmental biology, human physiology, and immunology. His excellence in teaching has not gone unnoticed and was officially recognized with the Mortar Board 1992 Excellence in Teaching Award.

He has an impressive array of findings during his research career at USC, all focused on developmental genetics and immunology. He was among the very first to isolate Y-specific DNA sequence from the mouse. He has investigated the genetic basis of strain differences in osmotic lysis of red cells, eye

development, hematopoesis kinetics, and cancer. He set up USC's first transgenic mouse facility and directed it for ten years. He has been involved in several projects using transgenic mice from this facility to investigate control of gene expression including alcohol dehydrogenase, alpha1-acid glycoprotein, the testes specific histone (H1t), globin and myolin basic protein. The alpha1-acid glycoprotein mice have been extensively used in drug disposition studies. Mike and his longtime collaborator, Dr. Gary Van Zant, have recently shown an effect of inbreeding and genetics on telomere length. In 1992 he became a member of the Stock Center Internal Oversight Committee, serving as the chair for several years. So when the Stock Center's founder, Dr. Wally Dawson, decided to retire these were the skills that made Mike so appealing as the new director.

Mike took on his new role as director in 2000 with enthusiasm and quickly began to push *Peromyscus* research forward. Under his direction a *Peromyscus* BAC library was constructed, and he has made significant advances in cryopreservation and artificial insemination in this genus. He has recently contributed to the understanding of imprinting in *Peromyscus* through collaborations with Paul Vrana and Shirley Tilghman. His biggest contribution, however, was obtaining funding for and overseeing the development of a medium-density genomic map. In pursuit of this goal, the Stock Center now has hundreds of microsatellite markers, thousands of expressed sequence tag markers, a radiation hybrid panel, and a backcross panel—all of which will advance *Peromyscus* research and are credited to Mike's efforts.

Mike officially retired at the beginning of September 2006, but is remaining in Columbia through December to help the new directors with the transition. He and his wife, Lorraine, have bought a house in Fort Collins, Colorado for their retirement. Retirement for Mike, of course, will be far from inactive. Mike is looking forward to finding a postdoctoral position so he can get back in the lab, and he will fill his free time skiing and hiking in what is arguably one of the most beautiful parts of the country. Perhaps most importantly, he will be near one of his favorite places, the Wind River Mountains in Wyoming. Mike Dewey is an intellectually curious and creative person. He is a person of unquestionable integrity with a cheerful and optimistic manner. We wish him luck and happiness. He will be greatly missed!

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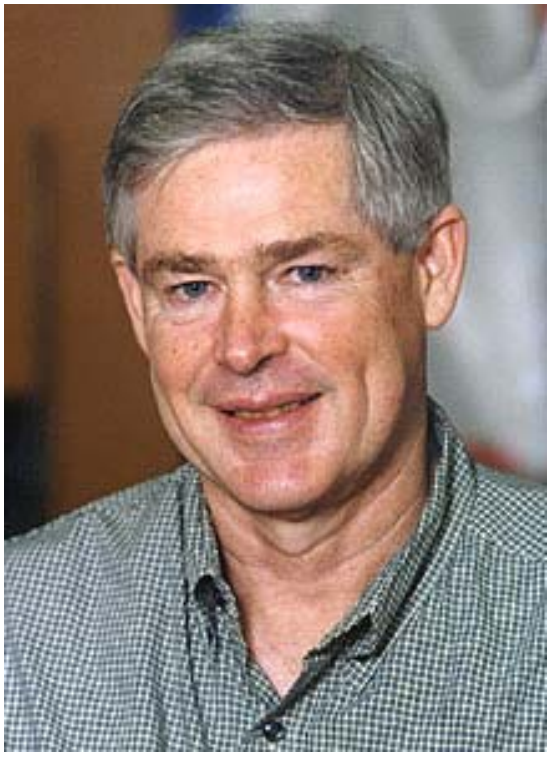
Meet the Director of the PGSC, Dr. Michael R. Felder

Dr. Michael R. Felder is the new Director of the *Peromyscus* Genetic Stock Center. Along with the new Associate Director, Dr. Gabor Szalai, he accepted the position this fall. Mike received his B.S. in biology from Stephen F. Austin State University near his hometown of Alto, Texas. He received his Ph.D. in genetics from the University of California at Davis in 1970. Following postdoctoral training at Michigan State University studying genetic control and biochemistry of maize alcohol dehydrogenases he became an Assistant Professor in the Biology Department at the University of South Carolina. He is currently Professor of Biological Sciences.



Mike's main interest has been in mammalian genetics concentrating on the alcohol dehydrogenases in mice and *Peromyscus*. He was the first to identify a mammalian alcohol dehydrogenase deficiency in the deer mouse and those stocks have been used to confirm the existence of alternative routes of alcohol metabolism. He collaborated with Wally Dawson mapping several enzyme encoding genes in the deer mouse. He has also collaborated with Mike Dewey in identifying control regions of the mouse *Adh1* gene using transgenic expression analysis. More recently he has been using transgenic over-expressing models to study the role of CYP2E1 in alcohol-induced pathology. Mike's main interest has always been regulation of gene expression primarily with the alcohol dehydrogenase and CYP2E1 genes as models. He is particularly interested in the *Peromyscus* gene mapping program and has plans to explore possible variation in alcohol-induced pathology among *Peromyscus* species and genetic variants.

Like Mike Dewey, Mike Felder enjoys the West, camping, and fishing. He is enthusiastic about this new challenge and looks forward to serving the *Peromyscus* community. He feels he is following two outstanding leaders of this facility, but is very excited about having his colleague, Gabor Szalai, as the co-Director. Both Mike and Gabor look forward to a further enhancement of the Stock Center.

♦♦♦♦♦♦♦♦♦

Meet the Associate Director of the PGSC, Dr. Gabor Szalai

Gabor Szalai grew up in a small town in Hungary. Although his father was a biology teacher, as a child he preferred physics, especially electronics and optics. The high school he attended did not have a physics club, so he joined the chemistry lab and gradually his interest turned towards chemistry. In 1985 he went to Colchester High School in Vermont where he took advanced anatomy and physiology classes taught by William Romond. He opened Gabor's mind to the chemical processes driving biology, especially molecular genetics.

After being a computer programmer for two years Gabor started his academic studies in bioengineering at the Technical University of Budapest (Hungary), earning his BSc in 1990 and his MSc in 1992. In1990 he received scholarship and spent one semester at the University of South Carolina working in Dr. Bert Ely's lab in the Department of Biological Sciences. From 1992 to 1995 he worked in Dr. Sandor Lazary's laboratory at the University of Berne (Switzerland) where he characterized the horse MHC class II loci and their allelic linkage to diseases, work for which the Technical University of Budapest awarded him a PhD in 1995.

For the next three years he was a postdoctoral researcher and assistant professor at the Technical University of Budapest, teaching several courses and pursuing research. His research interest was developing DNA based studies for food authenticity analysis. In 1999 he returned to South Carolina and worked in Dr. Michael Felder's lab as a postdoctoral researcher. He was interested in the mouse alcohol dehydrogenase (ADH) complex and its regulation. He came across deer mice for the first time during this work. He and Dr. Felder were able to identify two new mouse ADH genes using the *Peromyscus* ADH cDNA as a probe. In 2002 Gabor moved to Charleston, SC and worked at the Hollings Cancer Center in Dr. Dennis Watson's lab. He was studying several ETS transcription factors (Fli-1, Pdef) and their role in megakaryopoiesis and cancer using transgenic and knockout mouse models. Gabor has published numerous scientific papers, a book chapter on the MHC of the horse and a review article about megakaryopoiesis.

He accepted the position as the Associate Director of the *Peromyscus* Stock Center in August, 2006.

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THEREFORE…

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Major Histocompatibility Complex-Dependent Mate Preferences in Male *Peromyscus polionotus*

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Ryan and Lacy (2003) demonstrated biased behavior in male oldfield mice (*Peromyscus polionotus rhoadsii*) towards female mice based on very small kinship differences. Males in this unusually monogamous rodent species (Margulis 1998) preferred less-related females, with an average kinship difference of 1.3% between preferred and non-preferred females. Males subsequently mated with their preferred females showed higher reproductive success than males mated with non-preferred females (Ryan & Altmann 2001). The mechanism by which these male mice distinguished such small differences in kinship is not known. Previous work on house mice (*Mus domesticus*) has provided evidence that products of the major histocompatibility complex (MHC) can be used to discriminate among individuals, with mice often preferring MHC-dissimilar mates (reviewed in Knapp 2006; also see Spehr *et al.* 2006).

We investigated this potential mechanism by examining the relationship between allele-sharing at microsatellite loci within the MHC of *P. polionotus* mice and male preferences for females, using the same individual mice tested in Ryan and Lacy's study. Based on Ryan and Lacy's results, and assuming less-related mice share fewer MHC alleles, we predicted these male mice would bias behavior towards receptive and unreceptive females sharing fewer alleles at MHC microsatellites.

The *P. polionotus* mice used in this study were obtained from an outbred laboratory colony maintained by R. Lacy at Brookfield Zoo. The source and housing conditions for these mice, and the methods used to perform the social preference tests were described previously (Ryan & Lacy 2003). Briefly, in the choice trials a single male could approach and make limited contact with either of two females; either both in proestrus (receptive to mating) or both in diestrus (unreceptive). Time spent by a male near a female was used as the measure of his preference (Ryan & Lacy 2003).

DNA was extracted from mouse tails using Puregene extraction kits (Gentra Systems, MN). Three polymorphic microsatellites within the MHC Class Ib region of *P. leucopus,* also identified in *P. polionotus* (Eklund & Ober 2000), were then amplified in a small volume PCR. Class Ib products are expressed on

sensory neurons within the murine vomeronasal organ, and may aid in pheromone detection (Dulac & Torello 2003; Loconto *et al.* 2003). Forty-two males and 84 females were assigned genotypes at these microsatellites.

MHC sharing between a male and a female was assessed with respect to two measures of genetic similarity: allele sharing and haplotype sharing. The number of alleles shared between the male and each of the two females in a trial was determined at each of the three loci and then summed over the three loci. To measure haplotype sharing, we reasoned that mice sharing one allele at each of three loci likely shared a haplotype. Therefore, we categorized pairs based on whether the males shared at least one allele at each locus with the female or shared no alleles. Pairs that shared alleles at one or two loci, but not all three, were not scored.

In the analysis of allele sharing, a comparison between the diestrus and proestrus conditions showed a significant interaction between estrus stage and allele sharing, in which male time preferences for diestrus females sharing few or many alleles differed from preferences for proestrus females sharing few or many alleles (F = 8.471, df = 1, P = 0.006). Specifically, males spent significantly less time with proestrus females sharing four or more alleles than with diestrus females sharing four or more alleles (sq.-root transformed, right side data: t = 3.082, df =22, P = 0.005).

In the haplotype-sharing analysis, males tended to spend more time with diestrus females sharing a haplotype (Fig. 1: log-transformed data: t = 1.815, df = 18, P = 0.086). While also not significant, the opposite trend was apparent for males with proestrus females (Fig. 1; t = 1.227, df = 18, P = 0.24). When comparing diestrus to proestrus, time preferences based on haplotype sharing differed between the two estrus stages, and the interaction between estrus state and haplotype matching was significant (log-transformed F = 4.357, df =1, P = 0.044).

Ryan and Lacy (2003) reported that male *P. polionotus* preferred less-related females as potential mates, regardless of estrus state. Therefore, we expected that males would bias behavior towards both proestrus and diestrus females sharing fewer MHC microsatellite alleles. Our results partly supported this expectation, but suggest that the mechanism of kin discrimination used by these mice may be more complex than simple MHC use, as suggested by others (i.e., Hurst 2005). Our results did support previous results showing outbreeding mate preferences in estrus (or proestrus), but not diestrus, in *Peromyscus* (Keane 1990).

It is also interesting that male *P. polionotus* MHC preferences as measured by allele sharing were similar to those measured by haplotype sharing. Few studies have compared allelic to haplotype-based preferences, but one study in humans found haplotype-based MHC preferences, which were not

apparent when allele-sharing at individual loci was examined (Weitkamp & Ober 1998). More understanding of the mechanism for detection of MHC products may help to explain how these genetic differences are functionally interpreted (reviewed in Apanius *et al.* 1997; also see Spehr 2006, Dulac & Torello 2003).

To summarize, our results showed: 1) a change in male mate preferences for unreceptive females sharing many MHC alleles to receptive females sharing few alleles, and 2) a change in male mate preferences for unreceptive females sharing an MHC haplotype, to receptive females not sharing an MHC haplotype. This suggests that male *P. polionotus* are able to detect and discriminate among MHC-types, using both overall haplotype sharing and allele-sharing as markers. These data combined with Ryan and Lacy's results indicate that male *Peromyscus polionotus* choose less-related females as mates, but may not rely exclusively on MHC cues to make this discrimination. Further research is needed to determine the mechanism of kin discrimination and mate choice in these peromyscine mice.

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Acknowledgements

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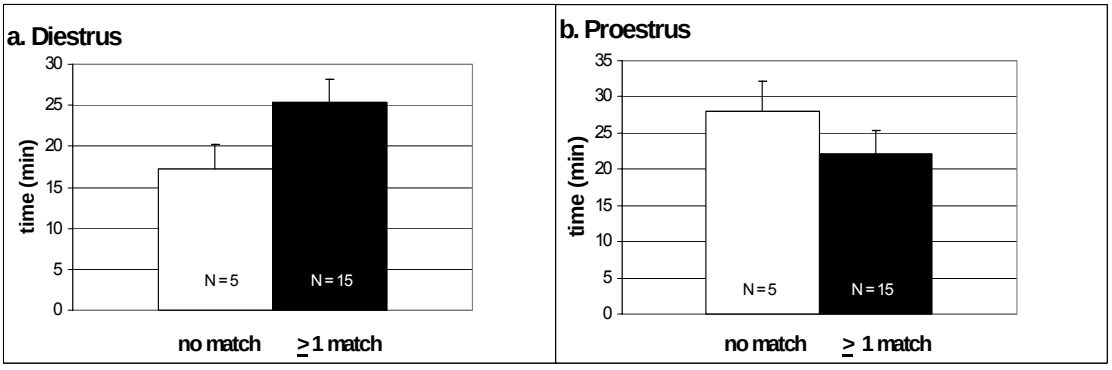
Figure 1. Haplotype sharing. Average time spent by males with females sharing no alleles at each locus (no match), or at least one allele at each locus (≥1 match), for diestrus (a), or proestrus (b) females. Standard error bars and sample sizes are shown. (Estrus stage x Haplotype-sharing interaction, p = 0.044).



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Biogeography and Population Genetics of *Peromyscus maniculatus* in the American West

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We currently have two active research projects involving *Peromyscus maniculatus*. Both projects involve examining population movement and demographics utilizing genetic data. One concentrates on the island biogeography of Washington's San Juan Islands, while the other examines a population boundary found in California and Oregon. Both projects are utilizing mtDNA sequence and microsatellite data.

The San Juan Islands archipelago has been heavily influenced by repeated cycles of Pleistocene glaciation, with the last recolonization occurring within the last 10,000 years. Under an idealized system of a single colonization event with a subsequent "island-hopping" pattern of intra-archipelago movement, it should be possible to determine the colonizing mainland population and the order in which islands were colonized. Using mtDNA control region sequence data we were able to reject the null model of a single colonization event. It appears that colonization occurred in multiple waves from multiple originating populations. Finally, Pacific Northwest mainland mice in general lack geographic structure, suggesting that high levels of gene flow persist between populations. Currently, we are examining data from microsatellite loci to see if we can gain further resolution.

Building off recent work in Yosemite National Park on *P. maniculatus* (D.S. Yang *et al*., in review), we are also exploring an apparent population boundary that exists between Pacific Northwest/Great Basin populations and California populations. We are able to define these populations based on highly divergent mtDNA haplogroups. Current work with microsatellite loci, on the other hand, reveals that the two major mtDNA haplogroups are actively breeding with each other, and that the presence of these two haplogroups is likely the result of multiple isolations of each population into refugia during Pleistocene glaciation events. Nevertheless, geographic structure of microsatellite genotypes exists in the area of the mtDNA boundary, which is what I am currently exploring.

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Natural Y Chromosome Variation Modulates Stress and Diabetic Phenotypes

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Blood glucose regulation is among the most critical processes in mammalian physiology. Consistently elevated blood glucose levels result in the disease Diabetes Mellitus (DM). The primary hormone preventing hyperglycemia is insulin. While environmental factors and obesity play a large role in inducing human DM, genetic factors also play a significant role. It has been proposed that variants underlying common human diseases including DM represent positive selection to past environments. This suggests that other closely related populations with differing ecological niches should also exhibit such variation.

We assessed ability to regulate blood glucose in two recently diverged species of *Peromyscus* which differ in several behaviors. Our data shows that males of these two species differ greatly in their ability to regulate blood glucose levels, and that this difference is largely mediated by differences in Y chromosome sequence. These findings have implications both for adaptive variation associated with different ecological niches and human disease. We suggest that studies of animals representing natural populations will yield insights not possible with mixed and/or inbred lines such as commonly used house mouse (*Mus*) lines.

Peromyscus polionotus is one of the few mammalian species documented to be monogamous in the wild, while its sister-species *P. maniculatus* has been shown to have multiple paternity within a litter. The insulin/insulin-like growth factor (Ins/Igf) pathways are key metabolic regulators of mammalian growth and behavior. Because they differ in post-natal growth, sexual dimorphism, mating system, and burrow complexity, we asked whether the Ins/Igf system might exhibit potentially adaptive variation between the two *Peromyscus* species. For example, monogamous males spend more time involved in parental care – such care would likely necessitate longer periods of fasting than in males engaged in less parental care.

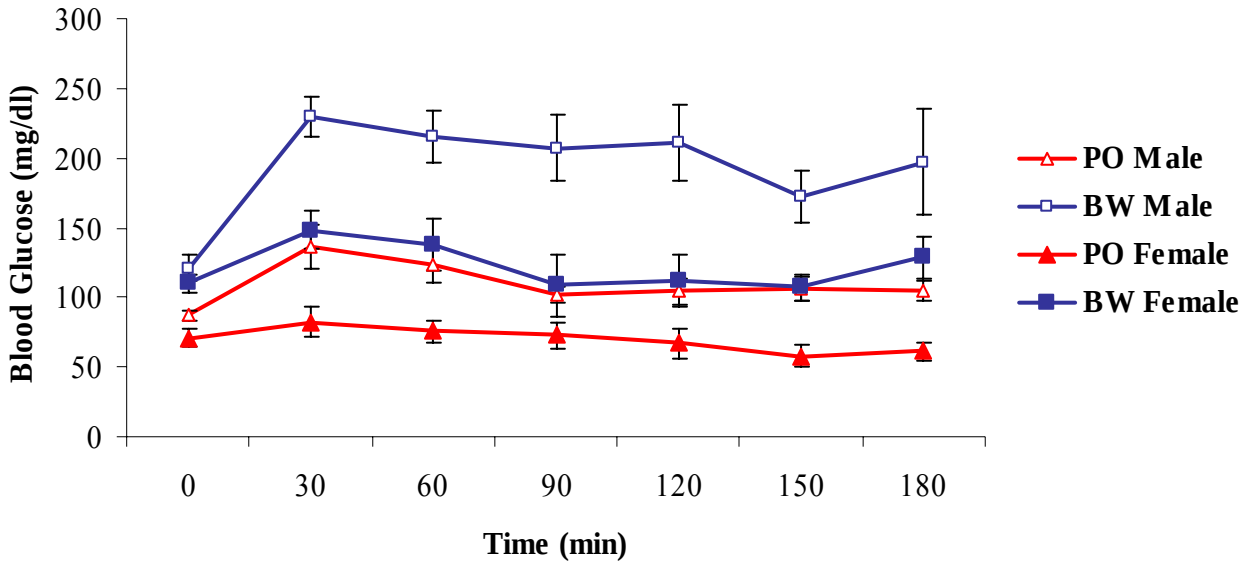
We first asked if the two species were equally adept at regulating blood glucose, the primary post-natal function of the insulin pathway. We performed

glucose tolerance tests (GTTs) on 15+ individuals of each sex from both species. These tests involve 18 hour fasting, then injection of glucose, and monitoring of blood glucose levels. We utilized the *Peromyscus* Genetic Stock Center strains PO (*P. polionotus*) and BW (*P. maniculatus*). Females of both species showed similar profiles and a return to normal blood glucose levels by 90 minutes. In contrast, males of the two species displayed highly divergent patterns: PO blood glucose levels rose little and returned to near baseline levels by 60 minutes, while BW levels rose much higher and did not return to baseline (Fig. 1).

We next performed GTTs on a strain of Y-chromosome consomic mice. These animals have been bred such that males are genotypically BW, with the exception of the Y chromosome which is of PO origin. Strikingly, these BW Y^{PO} animals showed a response more similar to that of the PO males than the BW males (Fig. 2). These data suggest that PO gene variants on the Y chromosome are largely responsible for the differences between males of the two species.

We also performed a sham GTT, in which males were fasted, and then injected with saline rather than glucose. PO male blood glucose levels were unaffected by the saline injection as predicted. Surprisingly, the BW male levels rose after the saline injection and again did not return to baseline (Fig. 3). These data show that these species differences in regulating blood glucose are largely due to a differential response to stress. We have also performed glucose tolerance tests on *P. polionotus leucocephalus* (PGSC strain – LS), representing a distinct population from that of the PO stock (*P. p. subgriseus*). The LS males show a similar GTT response to the PO males (data not shown), confirming the species difference. We feel these data are consistent with adaptive variation in *P. polionotus* males to a monogamous lifestyle.

Figure 1.



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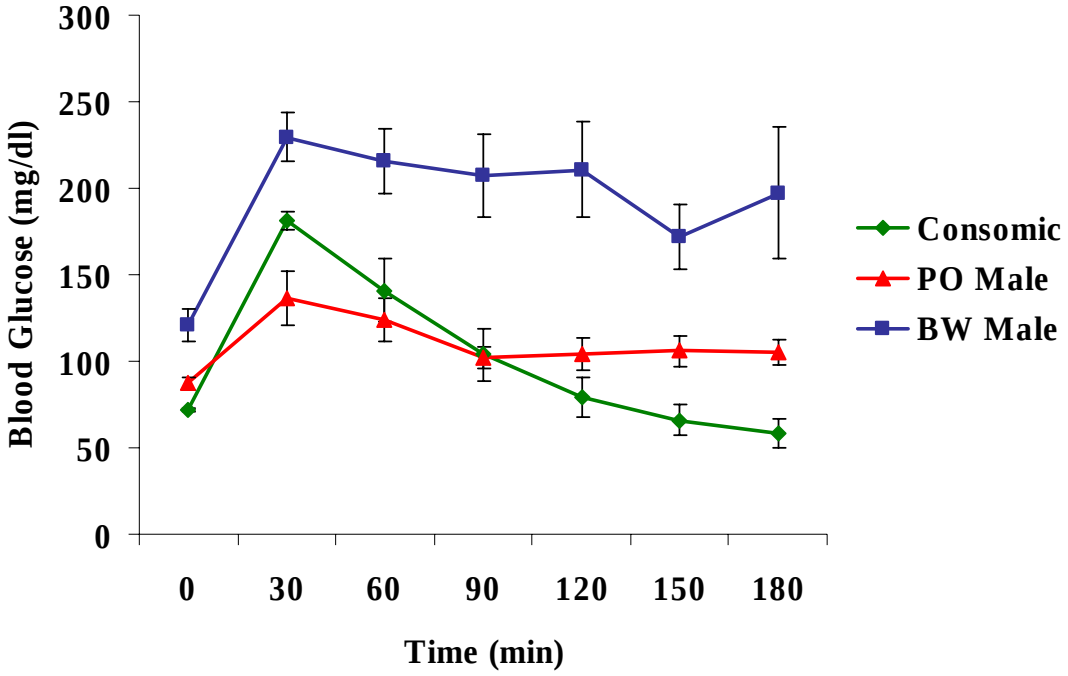
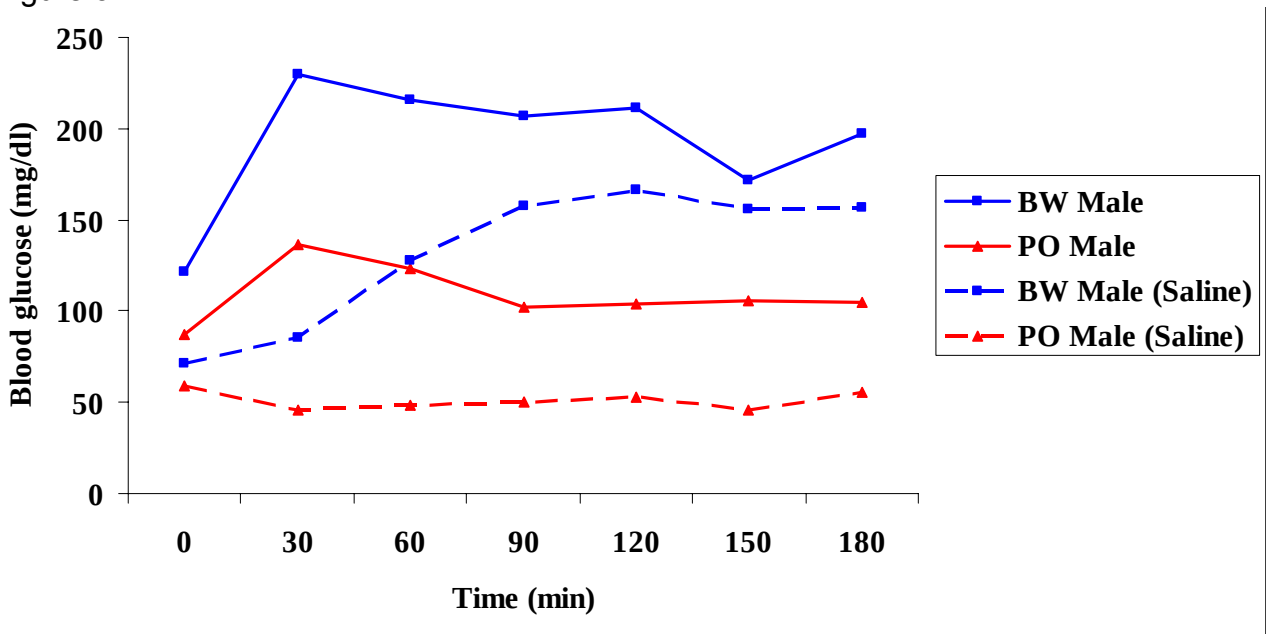


Figure 3.



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Mining the *Peromyscus* Genome: Early Returns from the First *Peromyscus* BAC Library

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The CHORI-233 *Peromyscus maniculatus rufinus* bacterial artificial chromosome (BAC) library was constructed at the Children's Hospital Oakland Research Institute. The library was constructed after a successful grant application from the *Peromyscus* Genetic Stock Center. The average size of inserted *Peromyscus* DNA in each BAC is ~ 180,000 base pairs. The large BAC insert size facilitates comparative genomics and identification of gene regulatory regions. BACs are identified by hybridizing a gene probe to filters containing individual clones in an identification grid.

As this is the first publicly-available *Peromyscus* BAC library, we probed filters to identify several genomic regions of import to the *Peromyscus* research community. Initial regions of interest coincided with the research interests of three laboratories: coat color genetics (Hoekstra lab, U.C. San Diego), hemoglobin population genetics (Storz lab, U. Nebraska), and genomic imprinting, X chromosome-inactivation, and placental development (our lab).

BAC filters (obtained from CHORI) were probed with 3-5 radioactively labeled DNA probes during any one hybridization. These probes were between 150bp and 1.4kb in length. Positive clones were further tested by PCR assays. Re-probing was only necessary for three regions of interest. Unambiguous clones were identified for all three after the second hybridization was performed. Currently we have identified and confirmed BAC clones representing the regions of interest listed in Table 1.

Table 1.

Probe	Mouse Syntenic Region	Research Interest	Lab
Agouti	Ch 2, 89.0cM	coat color genetics	Hoekstra
Mgrn1	Ch 16, 2.0cM	coat color genetics	Hoekstra
Mc1r	Ch 8, 68.0cM	coat color genetics	Hoekstra
Alpha-globin	Ch 11, 16.0cM	hemoglobin genetics	Storz
Beta-globin	Ch 7, 50.0cM	hemoglobin genetics	Storz
Snrpn	Ch 7, 28.65 cM	genomic imprinting	Vrana
Gtl2	Ch 12, 54.0 cM	genomic imprinting	Vrana
H19	Ch 7, 69.03 cM	genomic imprinting	Vrana
Peg3/Pw1	Ch 7, 6.5 cM	genomic imprinting	Vrana
Sgce	Ch 6, 1.0 cM	genomic imprinting	Vrana
Lit1	Ch 7, 69.3 cM	genomic imprinting	Vrana
Xist	Ch X, 42.0	X-inactivation	Vrana
Esx1	Ch X, 57.0	placental development	Vrana
Csh2	Ch 13, 14.0cM	placental development	Vrana

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Changes in Cell-Cycle and Extra-Cellular Matrix Gene Expression in *Peromyscus* Interspecific Hybrids

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Crosses between two species of *Peromyscus* have been shown to produce parent-of-origin specific growth and developmental defects. The hybrid defects are particularly pronounced in the placenta. *P. maniculatus* (strain - BW) females when mated to *P. polionotus* (strain - PO) males produce placentas half the size of the parental species, as well as growth-retarded embryos. In contrast, PO females mated to BW males result in embryonic and placental overgrowth, and deleterious phenotypes.

We took a global approach to assessing gene perturbations in the hybrid placentas by using *Mus musculus* cDNA microarrays. Signal strength was low due to divergence between the two genera. However, several thousand genes were suggested by ANOVA analysis to exhibit significant differences in expression levels between the parental strains and hybrids. Thirteen of seventeen genes tested to date by quantitative PCR have displayed the pattern suggested by the microarray analysis.

Two classes of genes stood out in the data analysis as being affected: those influencing the cell-cycle and extra-cellular matrix (ECM). Our work suggests that cell cycle regulators at the G1/S phase checkpoint are down-regulated in the large hybrid while the small hybrid is more variable. ECM genes are typically downstream targets of cell cycle regulation, and their mis-regulation is consistent with many of the dysmorphic phenotypes. Thus there appears to be an imbalance in proliferation in the mature placenta of the reciprocal hybrids. These trends appear to apply to embryonic as well as placental tissue. As an example, collagen gene expression is severely diminished in the hybrids (Figs. 1 & 2).

Figure 1. Assays verifying expression differences in ECM related genes. Quantitative real-time PCR assays were used for *Col1a2* (Procollagen I), *Col3a1* (Procollagen III), and *Pcolce* (Procollagen Enhancer). *Timp3* (Tissue Inhibitor of Metalloproteinase 3) RNA expression level was confirmed using semi-quantitative low cycle radioactive PCR. All samples include N ≥ 3.

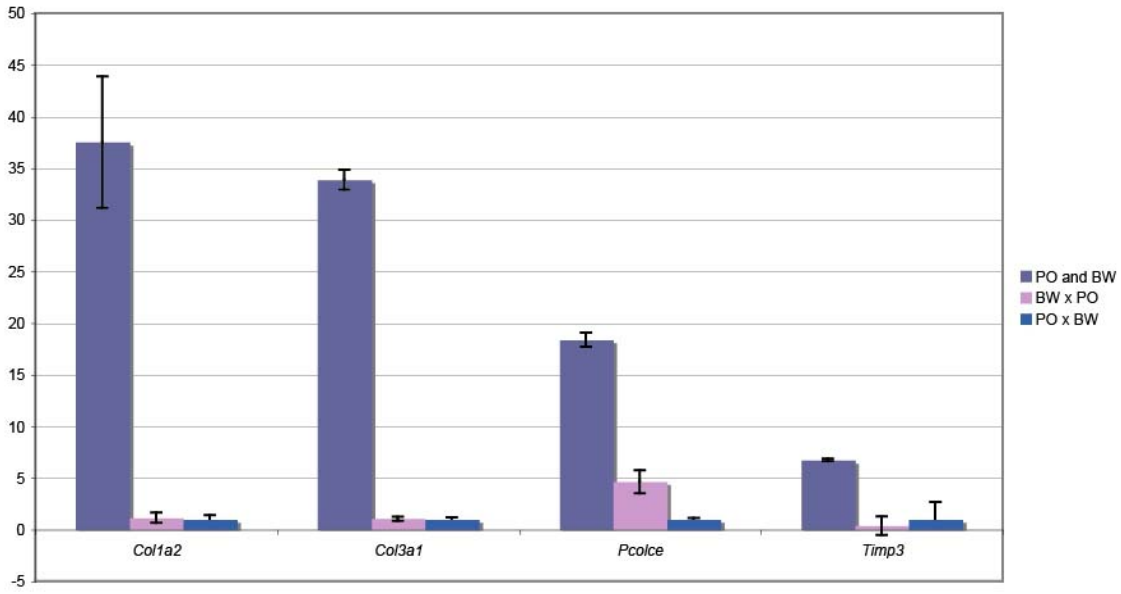
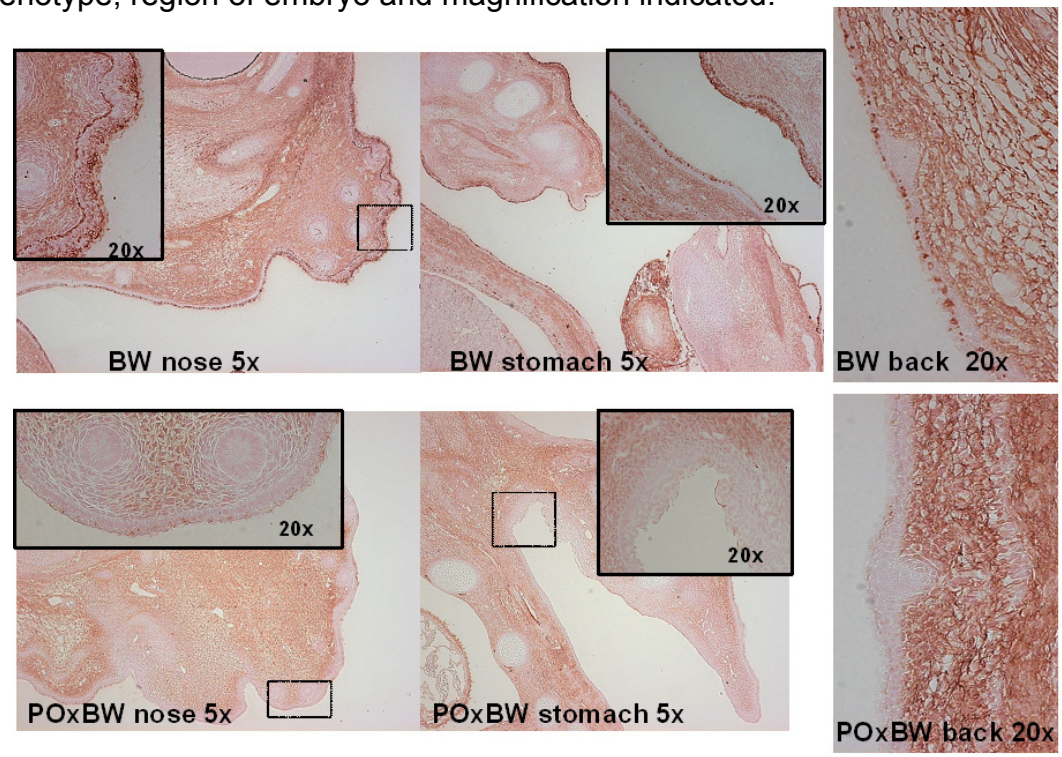


Figure 2. Staining of embryonic day e13.5 sections with a Collagen I antibody. Genotype, region of embryo and magnification indicated.



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Characterization and Transfection of *Peromyscus* Embryonic Fibroblasts (MEFs)

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Transgenic technology has not yet been developed for any *Peromyscus* species. The ability to manipulate gene expression would make *P. maniculatus* a more attractive system to biomedical researchers. In combination with its capacity for classical genetics, ecological, population, and behavioral studies, transgenic technology would make the *P. maniculatus* complex among the most complete biological study systems.

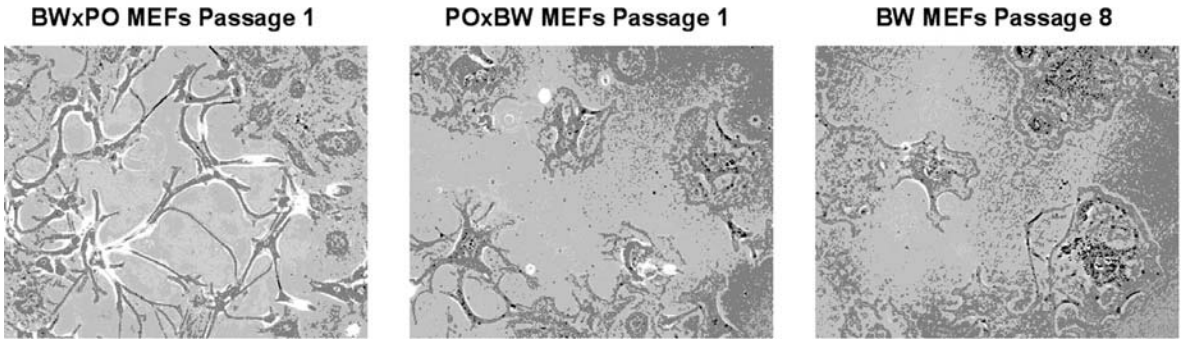
Development of transgenic embryos requires optimization of a number of reproductive techniques besides introducing foreign DNA into the zygotes. These procedures, which include retrieving the zygotes and transferal to pseudo-pregnant females, are potentially more difficult than the transfection itself. While we are currently developing these reproductive techniques, we are taking a complimentary approach by developing transfection approaches for *Peromyscus* cell lines.

Mouse embryonic fibroblasts (MEFs) are a relatively easy to culture cell-type, and primarily give rise to connective tissue, though they may also give rise to certain other mesodermal derivatives. We are optimizing transfection of *Peromyscus* MEFs for two reasons, both as an advancement of *Peromyscus* technology, and as a way to study gene expression changes occurring in hybrids of *P. maniculatus* (PGSC strain = BW) and *P. polionotus* (PGSC strains PO & LS). Recent work has shown that genes involved in extra-cellular matrix formation (e.g. collagens) exhibit altered expression in the hybrids. Temporal expression profiles of extracellular matrix proteins are recapitulated in MEFs, making them an attractive system to study the hybrid dysgenesis at the cellular and molecular levels. We are currently optimizing transfection techniques using murine stem cell virus vectors containing green fluorescent protein (GFP).

We have cultured MEFs from the LS, PO, and BW strains. We have also cultured MEFs from PO female x BW male hybrids (which display somatic overgrowth), and BW female x PO male hybrids (growth retarded). The pure strain MEFs appear comparable in morphology and proliferation. However, the PO x BW lines exhibit altered morphology and display apparent premature senescence compared to MEFs derived from undersized BW x PO hybrids

(Fig.1). Further investigation is warranted to explain this differential MEF morphology.

Figure 1. Morphology of *Peromyscus* MEFs. Genotype and passage number are indicated. BW x PO hybrid MEFs at passage 1 resemble those of both parental strains at the same passage. The PO x BW MEFs exhibit altered morphology more comparable to older (passage 8) BW MEFs.



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Utility of Affymetrix GeneChip Technology as a Platform for Transcriptome Analyses Within Peromyscines

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Various platforms for DNA microarrays, including oligonucleotide and cDNA chips, have enabled global transcriptome comparisons between multiple tissue types to delineate patterns of differential gene expression. Development of species-specific platforms is a labor-intensive and costly process, often limited to the subset of cDNA and/or EST sequences that have been fully annotated for any one species. Affymetrix, Inc. produces a robust platform of high-density oligonucleotide arrays that include >22,600 probe sets representing >14,000 different transcripts and/or transcript variants (Mouse Expression GeneChip® 430A 2.0). This technology, however, has been limited as a general platform for transcriptome analyses due to the small number of species for which GeneChips® are commercially available.

The mRNA target sequences that comprise the GeneChip® platform are each represented by a probe set that is composed of 11-20 probe pairs. Each probe pair consists of two 25-mer oligonucleotides, one of which is a perfect match (PM) to the target sequence while the other is a mismatch (MM) designed with a mutated homomeric nucleotide for the middle (13th) base. The relative abundance of a particular transcript is defined by signal intensities, derived from analyses of differences between PM (target hybridization) and MM (background hybridization) across an entire probe set. Signals are then broken down into "present" (P), "marginal" (M) and "absent" (A) calls based on the significance (*P* value) for any PM-MM analysis (GCOS, Affymetrix). While the PM-MM system has been shown to produce significantly reliable analyses of mRNA pools across tissue types from species for which GeneChips® are available, the ability to detect a large pool of transcripts between different mouse species in cross-species analyses has yet to be determined.

In an effort to define the utility of this platform for transcriptome analyses across other murine and peromyscine species, and subsequently across various tissue types, we performed >80 hybridization experiments using the Mouse

Expression Array 430A 2.0 GeneChips®. Initial experiments involved the use of various tissue types, including whole brain, brain subregions, placenta and fibroblast cells from various strains of *Mus musculus* (CD-1, C3H, InX1h, C57BL6/J, *Paf*). These arrays averaged >60% P calls, an expected hybridization efficiency for this platform. *Mus caroli* fibroblast samples were used in hybridization experiments to define the validity of this platform within other murine species. *M. caroli* and *M. musculus*, while G-band identical, diverged approximately 5-7 mya (Silver 1995). However, P calls on the mouse array platform remained high for this species, averaging 49.43%. As part of our ongoing research into hybrid dysgenesis and placental dysplasia, reproductive isolation and rapid gene evolution manifest within the mammalian placenta, we analyzed mid-gestation placentas from *M. musculus* CD-1, *Mus caroli* and *Mus musculus x Mus caroli* hybrids. P calls for these samples averaged 57.63%, 50.70% and 57.75%, respectively, collectively indicating robust validity for detecting mRNA gene expression differences with this platform.

Our studies of placental dysplasia, imprinting incompatibility and rapid gene and retroviral evolution within the placenta have been intensely focused on studies between two *Peromyscus* species, *P. maniculatus* (BW) and *P. polionotus* (PO). Full descriptions of analyses of these datasets, including qRT-PCR (quantitative real-time RT-PCR) validation, sequence analysis and expression profiling are currently under manuscript review and have thus not been included here. However, we show P calls for these arrays, including analyses from neonatal testes and mid-gestation placentas, to illustrate the effective hybridization efficiencies for peromyscine mRNA pools on the mouse GeneChip platform. As shown in Figure 1, neonatal testes hybridization experiments average 22.73% (BW) and 23.20% (PO) while placenta hybridization experiments average 19.87% (BW) and 20.20% (PO). Hybrid placentas produce higher P calls, due largely to aberrant gene expression, averaging 22.60% (BW x PO) and 22.30% (PO x BW).

In collaboration with the *Peromyscus* Genetic Stock Center, we aim to define and characterize aberrant gene expression profiles in a metastatic hardarian gland tumor model within *P. leucopus*. Hybridization efficiencies with these samples were comparable to those obtained with PO and BW samples, averaging 20.40% across all normal hardarian gland mRNA samples from *P. leucopus*, 20.25% across strain 109 (the tumor susceptible strain) hardarian glands, 22.10% across strain LL (a non-tumor susceptible strain) hardarian glands, and 25.30% from 109 hardarian gland tumors (Figure 1). Further validation and characterization of these datasets are currently underway.

Previous work in modifying the GeneChip® platform for cross-species analyses has been limited to human vs. non-human comparisons, including other primate species (Chismar et al. 2002), pig (Shah et al. 2004), cow (Ji et al. 2004) and canine (Grigoryev et al. 2005). In the latter analysis, 14% hybridization efficiency was obtained from standard P calls for canine mRNA pools on human

GeneChips®. It is clear from these analyses, and our own, that the PM-MM system of filtering a probe set from any cross-species hybridization experiment may incorrectly assign an absent (A) call to a particular probe set. This may be due to either lower PM hybridization or higher MM hybridization efficiency across a subset of the 11 probe pairs of a set due to sequence divergence between the GeneChip® target sequence and the hybridizing mRNA pool. Further work deconstructing probe sets is currently being explored in an effort to increase the range of informative target sequences from ~2800 mRNA sequences to >6500 for hybridization experiments with peromyscine samples. It is clear from these analyses (Figure 1), and the data obtained therein (not included), that the GeneChip® platform, while proving less informative for this group of mammals than for murine species, provides an informative amount of data regarding transcriptome variation between peromyscine species and tissue types. *For protocols for adapting this platform for analyses of gene expression within peromyscines, please contact R. O'Neill.*

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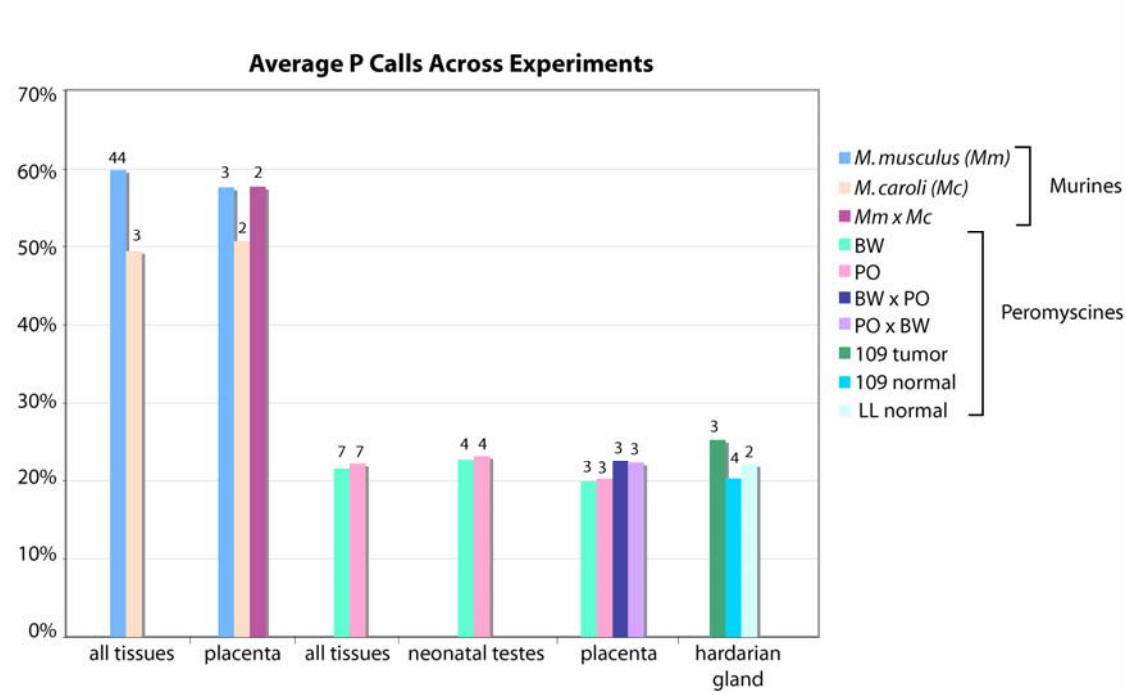
Figure 1. Graph of Average P calls derived from hybridization experiments of various mRNA samples to the *Mus musculus* array. The tissue type is listed on the X axis while the average is shown on the Y axis. Species and hybrids are indicated on the right. The number of replicates is indicated above each bar within the graph.



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Systematics and Phylogeography of Insular White-Footed Mice (*Peromyscus leucopus*) in Northeastern North America

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Systematics

Multivariate morphometric and mitochondrial (mtDNA) nucleotide sequence analyses were conducted on 25 populations of *Peromyscus leucopus* representing the eastern North American range of the species. An hypothesis of presence of previously unknown northeastern glacial refugia in the vicinity of George's and Brown's Banks, which served as colonizing sources of extant northeastern insular populations, was tested using combined morphological, nucleotide sequence, paleoclimatological, paleovegetational, geological, and geographical data sets.

Nucleotide sequence variation in the mtDNA control region was analyzed in 99 individuals representing 23 populations (nine insular, 14 mainland) from Nova Scotia (CA) to Georgia (U.S.A.). Distance and Maximum Parsimony-based phylogenetic analyses were conducted on 895 bp of mtDNA control region nucleotide sequence data to assess genetic variation within and among northeastern insular and eastern United States coastal mainland populations. Among the 23 populations sampled, 59 haplotypes were identified of which 26 were endemic to insular populations. Although there is limited evidence for phylogeographic structuring, interdigitation of haplotypes among populations suggests recent interchange of mitochondrial lineages. Analysis of mismatch distribution of pairwise haplotype frequencies indicates recent expansion for mainland populations, and a pattern of allopatric stability for insular populations.

Canonical variates, hierarchical cluster, MANOVA, and ANOVA analyses for 31 mensural characters were conducted on 1,340 wild caught, adult specimens of *P. leucopus* from 25 insular and mainland populations distributed from Nova Scotia (CA) to North Carolina (U.S.A.). Analyses indicate latitudinal clinal variation in size of external characters for mainland populations, and to a lesser extent for insular populations from southern New England, consistent with Bergmann's Rule. Patterns of craniometric variation among insular and

contiguous mainland populations exhibit significant variability that is overall inconsistent with observed latitudinal clinal variation for external characters. Geographic variation of craniometric and external characters among northeastern insular populations reveals a complex pattern of mosaic evolution.

Phylogeography

Interpretation of combined morphological, molecular and bathymetric data sets does not support the hypothesis for existence of northeastern Pleistocene glacial refugia, in the vicinity of George's and/or Brown's Banks, as colonizing sources for extant northeastern insular populations. Phenotypic and nucleotide sequence divergences among contiguous mainland populations reveals clinal differentiation resulting from late Pleistocene (Wisconsin)/Holocene northward migration along the coastal mainland and emergent coastal plain from southeastern United States Pleistocene refugia. Insular populations are Holocene coastal plain relicts, isolated by vicariance on topographic high spots that became islands in the northeast. Differentiation of insular populations is the result of a combination of genetic drift due to initial founding events and subsequent lack of gene flow resulting from isolation by rising sea level (up to 8,000 years for some populations), and localized insular phenotypic adaptation to variable environmental selective pressures during the Holocene.

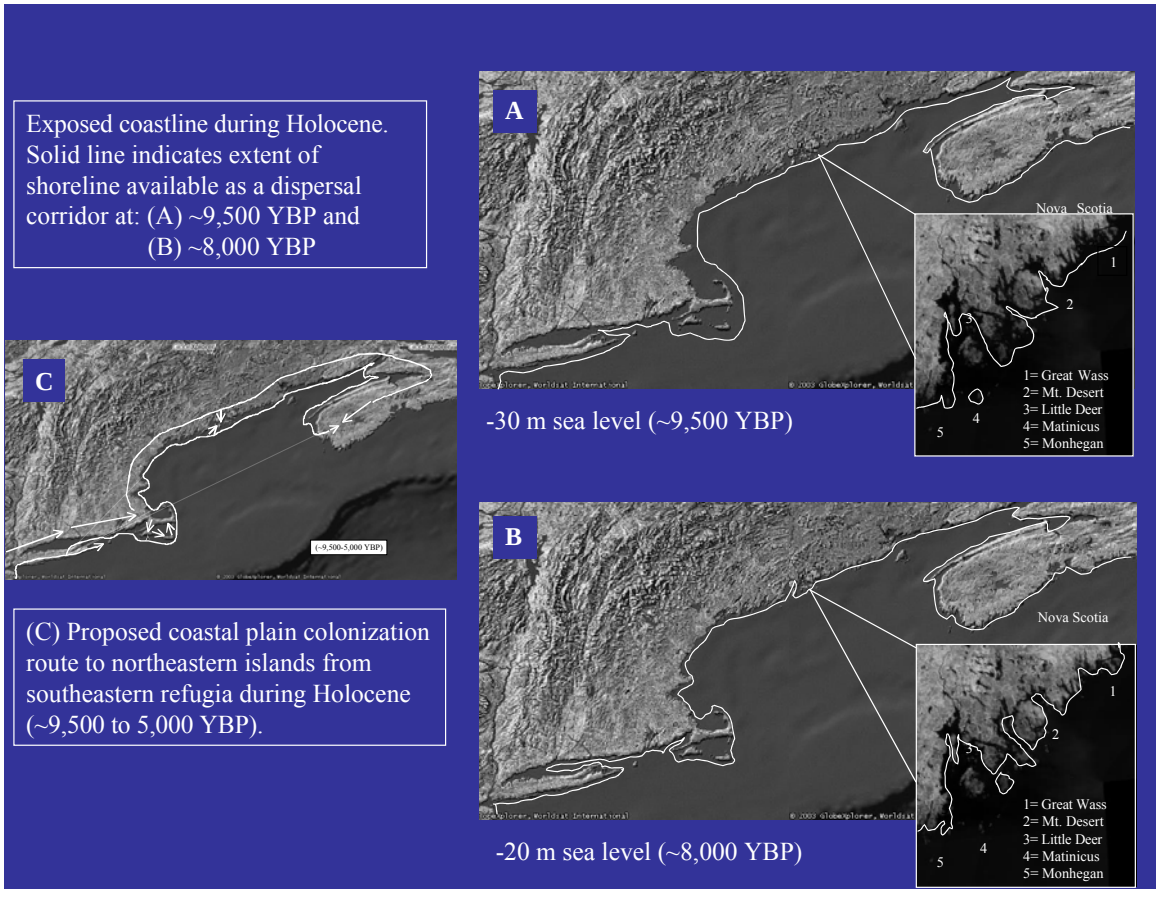
Taxonomy and Conservation

Based on morphological comparisons, *P. leucopus* is divided into four subspecies in northeastern North America. Current classification schemes (Carleton 1989; Hall 1981) recognize: *P.l. noveboracensis*, the mainland form which also occurs on coastal islands in the Gulf of Maine, Block Island, Rhode Island, and Long Island, New York; *P.l. caudatus*, endemic to Nova Scotia; *P.l. ammodytes*, endemic to Monomoy Island, Massachusetts; and *P.l. fusus*, endemic to Martha's Vineyard, and questionably to Nantucket Island, Massachusetts.

The subspecific status of *P.l. fusus* occurring on Martha's Vineyard Island, Massachusetts is considered valid, with additional inclusion of the population on Nashawena Island, Massachusetts. *Peromyscus leucopus* occurring on Nantucket Island, Massachusetts is sufficiently differentiated, morphologically and molecularly, from both Martha's Vineyard and adjacent mainland populations to warrant recognition as a separate subspecies and should no longer be assigned to *P.l. fusus*. The population occurring on Block Island, Rhode Island is sufficiently differentiated to warrant further consideration as a separate subspecies. The population on Monomoy Island, Massachusetts, sampled prior to reconnection of this island with the mainland, is morphologically distinct. This confirms its previously established taxonomy as a separate subspecies, *Peromyscus leucopus ammodytes*. However, because of periodic breakdown of physical isolating mechanisms during the last century, additional morphological

and nucleotide sequence analyses are required to assess its current taxonomic status.

In recent conservation literature there is abundant emphasis on designation of sub-portions of species as Evolutionarily Significant Units (ESU) for conservation and management practices (Crandall et al. 2000). Ryder (1986) defined ESU as: (1) a set of populations that is morphologically and genetically distinct from other similar populations; (2) a set of populations with a distinct evolutionary history. Moritz (1994) constrained the definition by emphasizing reciprocal monophyly for mitochondrial haplotypes. Based on morphological and mtDNA control region sequence data derived from this study, *P. l. fusus* fulfills the criteria required for consideration as an ESU. In addition, due to the shared biogeographic history of colonization and isolation, and observed morphological and genetic differentiation of insular populations on Nantucket and Block Island, consideration as ESU's is also warranted.



Acknowledgements

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Lyme Disease Vector Ecology Studies in New York State: Effectiveness of the Kness Snap-E® Trap

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As part of the vector ecology component of a three-year Lyme disease study, we collected small mammals from twelve counties along two transects of New York State to test ear tissue for the presence of the etiologic agent of Lyme disease, *Borrelia burgdorferi*. There is little published data evaluating snap-traps for this type of study, although many small mammal population ecology studies have utilized snap-traps, especially wooden-based Victor® or Museum Special traps. We examined the effectiveness of the uniquely designed, plastic-based Kness Snap-E® trap for collecting target mammals, primarily white-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculatus*), in seven of the twelve study sites for the 1998 season. The study sites were located in the Champlain basin from near the Canadian border (Clinton County, NY), to the lower Hudson Valley (Dutchess County, NY). The study sites ranged from areas of recent disturbance to typical old growth forests, and most were located on state-owned land such as wildlife management areas and state parks.

Previous studies citing the effectiveness of snap-traps used either Victor® or Museum Special (The Woodstream Corp., Lititz, PA) mammal traps (Galindo-Leal 1990, Martell 1979, Wiener and Smith 1972). The Snap-E® trap (Kness Mfg., Albia, IA) was chosen for this project for several reasons. Unlike the wooden-based Victor® or Museum Special snap traps, it has a heavy polystyrene base that is resistant to wet field conditions and cleaning. Its unique design employs a strong spring and heavy-duty plastic-coated stainless steel wire bail that is designed to travel 90 degrees from the base when triggered (rather than 180 degrees, as with other traps). In addition, the trap has a pre-formed bait cup surrounded by a large (35mm x 40mm) paddle-like trip mechanism (Fig. 1). Furthermore, when purchased in bulk, the cost of a Kness Snap-E® trap is less than one-fifth the cost of a Museum Special trap. We found no published data evaluating snap traps for the collection of small mammals for the assessment of tick- and other arthropod-borne infections. Therefore, the purpose of this study, based on the 1998 collection season, was to determine the effectiveness and efficiency of the Kness Snap-E® trap in the capture of small mammals, especially *P. leucopus* and *P. maniculatus*, and its usefulness for similar projects.

A total of 7364 traps baited with peanuts were set between May and October, capturing 813 small mammals. The Snap-E® trap was effective at capturing mostly *Peromyscus* species and short-tailed shrews but also captured a variety of other rodents and insectivores, including jumping mice, flying squirrels, chipmunks, voles, and smaller shrews. Most mammals captured were found dead in the trap (97.5%). Four non-target animals (birds and amphibians) were captured.

In general, the trap was effective for our study purposes. However, the dark color of the trap made it difficult to see in field conditions. The authors recommend tying fluorescent survey tape to the traps when setting. We concluded that the Snap-E® trap is an effective, reusable field tool for capturing small mammals, especially *Peromyscus* species, for the purpose of harvesting ear tissue for detection of *Borrelia burgdorferi* spirochetes. The trap may also be valuable for other studies involving the collection of small mammals.

Figure 1. The Kness Snap-E mouse trap. Photo taken from www.kness.com

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Production of Ultrasonic Vocalizations by Wild *Peromyscus*

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Ultrasound is commonly used by a diverse array of mammalian taxa, including bats, odontocete whales, insectivores, and rodents. Ultrasonic vocalizations (USVs) in these groups range from simple broadband clicks produced by whales, insectivores, and some megachiropteran bats, to highly modified, tonal signals that show structured change over time as in microchiropteran bats (Thomas et al. 2004). Ultrasound is mainly used for orientation and prey localization; however, these signals may also have social functions, including communication of individual identity or group membership, kin recognition, information transfer, mother-infant communication, mate attraction, and territorial defense (e.g., Kazial et al. 2001; Pfalzer and Kusch 2003; Yurk et al. 2002). In contrast to our wealth of knowledge on the use of USVs by bats and whales, we know comparatively little about the use of USVs by rodents in the wild (but see Wilson and Hare 2004). As with other mammalian behavioral systems, there has been extensive research on rodent ultrasound in the laboratory (Wolff 2003), where USVs have been documented for a number of rodent species, particularly within the superfamily Muroidea (Geyer and Barfield 1979; Hahn and Thornton 2005; Sales and Pye 1974; Sewell 1970). Despite the valuable and extensive research on USVs in rodents in the lab, it is unclear if and/or when, these USVs are produced in the wild, and how they function in natural habitats. Moreover, muroid rodents are regularly used as models for mammalian behavioral systems however, our understanding of how they use acoustic communication in the wild is extremely limited.

The genus *Peromyscus* is an ideal group within which to study USVs in a natural context especially given the extensive variation in the ecology and behavior of *Peromyscus* in the wild. Recently we attempted to systematically record *Peromyscus* producing USVs in the wild. We attempted these recordings at the Hastings Natural History Reserve in Monterey County, California where there are long-term live-trapping grids set up for the ecological and behavioral study of *P. californicus* and *P. boylii*. First, we live-trapped mice to determine the locations of resident individuals. After determining the location of resident individuals we recorded USVs by establishing a grid of up to 24 microphones capable of recording broadband sonic and ultrasound directly to sound recorders. Recording systems were set at sunset and retrieved the following morning. Over 6 nights, we recorded a total of 65 high quality, independent USV recordings. It was possible to determine which individuals and species were producing the

USVs based on home range analysis of trapping data and we found that both species produce USVs in the wild.

To understand the significance of these recorded USVs it is important to go over some terminology. A “syllable” is defined as a single discrete sound. A “phrase” is defined as a succession of syllables. A “motif” is a sequence of syllables that were recorded repeatedly over time and that were statistically predictable based on acoustic characteristics of the syllables, the number of syllables in a phrase, and the duration of time between syllables within a phrase. All of our recorded phrases fell into one of seven motifs—that is, there is a repertoire of approximately 7 USV motifs (or types) that are being commonly produced by wild *Peromyscus*. These results were recently published in *Frontiers in Zoology* (Kalcounis-Rueppell et al. 2006). If you would like to learn more about the USVs produced by these two species of *Peromyscus*, I encourage you to read the article and visit the open access article site (http://www.frontiersinzoology.com/content/3/1/3) because there are links to the acoustic files (that you can listen to) and figures of the spectrographs (frequency vs time) of the 7 USV motifs that we recorded.

To validate our field recordings and understand the extent of USV production in *Peromyscus* I visited the *Peromyscus* Stock Center to passively record USVs from captive cohorts of *Peromyscus* species using the same equipment that we used in our field study. We are still analyzing our data from the *Peromyscus* Stock Center and look forward to communicating the details to you in the future. For now, it is clear from our work at the *Peromyscus* Stock Center that our recordings from the field were produced by *Peromyscus*. Furthermore, it is clear from work at both the *Peromyscus* Stock Center and from the field at the Hastings Natural History Reserve that USV production is a common and underappreciated component of the behavior *Peromyscus*.

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Phylogeny and Behavior in Peromyscine Mice: a Developing Model of Vocal Signaling

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Stereotypic vocalizations occur in many mammals and possess characteristics thought historically informative. Evolutionary patterns are confounded however, by a paucity of appropriate phylogenetic hypotheses, as well as inadequate sample diversity. The muroid subfamily Neotominae comprise a diverse and monophyletic assemblage of 16 genera and approximately 120 species of rats and mice distributed broadly across North and Central America (Musser and Carleton 2005). This group subsumes a large and important species assemblage known generally as the peromyscine mice, which are in essence *Peromyscus* and its close relatives. While many phylogenetic schemes have been proposed based on morphological characters and mitochondrial DNA, systematic relationships within this group remain inadequately resolved (Bradley et al. 2004; Carleton 1980; Engel et al. 1998; Hooper and Musser 1964; Patton et al. 1980; Reeder et al. 2006; Rogers et al. 1984; Rogers et al. 2004; Stangl and Baker 1984).

Difficulties in discerning the phylogeny are similar to those of the Rodentia as a whole due to "their great numbers, their marked mutability and variability, their spread over almost every conceivable environment, their remarkable adaptability, the shortness of their generations, [and] their unusual fertility with overpopulation and severe mortality" (Simpson 1945:197) . Yet these very same characteristics allow this broad assemblage to become a useful model for testing a variety of ecological and evolutionary hypotheses.

Peromyscines are speciose, representing varied ecological and social conditions, and include at least four genera known to produce simple-to-complex stereotypic vocal signals. We chose this group to examine principal factors thought to influence the evolution of vocal communication. We analyzed both nuclear and mitochondrial sequences (inter-photoreceptor retinoid-binding protein, growth hormone receptor, and cytochrome B) among a comprehensive set of taxa representing all major lineages within peromyscines using Bayesian and Parisimony approaches. Concomittantly, we also recorded the stereotyped vocalizations in taxa representing the primary phylogenetic lineages in peromyscines.

Preliminary phylogenetic interpretations are congruent with current classifications in both membership and cohesion of the major tribes (Musser and Carleton, 2005). However, work in progress also recovers some novel relationships among deeply rooted lineages, as well as defines the sister groups to both *Peromyscus* and *Reithrodontomys,* and circumscribes the scope of *Peromyscus*. *Peromyscus* is paraphyletic if the majority of genera separated from it by Carleton (1980) are retained. Preliminary behavioural results reveal a large number of peromyscine taxa produce vocalizations that are repetitive, high amplitude, and characterized by a use of frequency that, collectively, includes a wide bandwidth of the acoustic spectrum, ranging from audible to ultrasonic (Fig. 1). Figuring prominently in our data are species recorded at the *Peromyscus* Genetic Stock Centre, and at a satellite colony housed at the University of Toronto, Department of Ecology and Evolutionary Biology. There are several distinct acoustic motifs among peromyscines, data which we are currently mapping and interpreting against our molecular phylogeny.

Figure 1. A male *Scotinomys teguina*, a peromyscine rodent, responding to the background vocalization of another *Scotinomys teguina* individual. Photos by Jacqueline Miller.

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