The Signal

Monthly newsletter of the W. M. Keck Center for Behavioral Biology at North Carolina State University
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Reade Roberts Receives Beckman Young Investigator Award

The Beckman Young Investigator (BYI) Program is intended to provide research support to the most promising young faculty members in the early stages of academic careers in the chemical and life sciences particularly to foster the invention of methods, instruments and materials that will open up new avenues of research in science.

Reade Roberts was one of seven named 2014 Beckman Young Investigator by the Arnold and Mabel Beckman Foundation, Irvine, CA, based on his proposal "A novel genetic model of dietary response and host-microbiota interactions", and a competitive presentation and interview. Reade was also recently honored at the annual Beckman Symposium in Irvine.

The seven 2014 Beckman Young Investigators span materials science, chemistry, instrumentation development, and biochemistry. Reade's innovative vision is the development of African cichlid fishes as a model system to understand the evolution, development, and genetic basis of gastrointestinal traits including host-microbiota interactions.

There is intense study of interactions between intestine and microbiota now in humans, mice, and zebrafish, but relatively few host genetic variants have been identified, and those that are known are largely Mendelian disease genes or artificial mutants - not really natural background variation. There has also been some work across broad taxonomic scales (all mammals, for example), but the evolutionary distance precludes any functional or mapping work.

The cichlid model fills a gap in the current set of models. Malawi cichlids provide the best of both worlds, since they diverged across trophic levels but remain inter-fertile to allow hybrid mapping crosses. The cichlids also have greater variation than traditional model organisms. Reade's preliminary data show drastic, predictable differences by genus in gut length, intestinal histology, and gut microbial communities. These traits are modulated by diet, but the effect of genus is much stronger. Reade will use hybrid mapping families plus comparative population genomics to pinpoint genes modulating intestinal development and homeostasis, and host genetic factors influencing colonization by gut microbiota.



Reade Roberts

When asked how Reade saw his chances of receiving the Beckman Young Investigator Award, he responded "As an evolutionary geneticist I was definitely at the

far biological end of the spectrum of research they support! It seems many of the BYI awardees made significant changes in their research focus during their careers, and combined these different skill sets into something novel. In my case, it was combining my model organism perspective and gastrointestinal focus from my Ph. D. work in mice with evolutionary genetic strategies I developed during my post-doc to study non-gastrointestinal traits in cichlids."

Reade's goal is to identify evolved genetic variants modulating dietary adaptation, as a way to identify novel genes and pathways involved in pathological response to diet in humans (*e.g.*, undernourishment, obesity, metabolic syndrome - the most widespread health issues globally). Thus, Reade's project applies his skill set to a completely new suite of traits with great relevance to human health, exactly what a Beckman Award is intended to achieve.

Evolution 2014



The 2014 Society for the Study of Evolution Meeting was held in the Raleigh Convention Center. This year, it was a combined meeting of the Society for the Study of Evolution, the Society of Systematic Biologists, and the American Society of Naturalists. The conference was attended by a large contingent of NCSU Keck Center members. Here are some of their impressions:

Jeremy J. Heath

This was one of the best meetings I have ever attended, thanks in large part to Allen Rodrigo and the organizing committee. Dr. Rodrigo, Director of NESCent (the National Evolutionary Synthesis Center) and head of this year's organizing committee, pulled off a great meeting. The breadth of topics was large enough to maintain interest and the venue was just the right size to allow a timely jaunt between talks. The breaks between organized sessions were optimized to allow planning for the next session or to catch up with old friends or meet new ones. Overall, a great meeting!

For me, the highlight was the ASN Presidential Address given by Dr. Trevor Price. Price unapologetically touted a recent paper he co-authored with Dr. Russell Lande and lead author Dr. Maria Servedio entitled, "Evolution of displays within the pair bond." In this paper, Servedio develops a population genetics model to unravel the enigma of continued mutual elaborate displays within the pair bond of socially monogamous animals.

Elaborate courtship display is presumed to be maintained by strong sexual selection, but in some species these displays continue after the pair bond has formed and manipulative experiments have indicated that these displays alter offspring provisioning by the receiving partner. Species with this kind of interaction include great grebes, yellow-legged gulls, zebra finches, and rock sparrows. It is difficult to imagine how sexual selection might maintain display beyond that used in the initial pair bond. Servedio's model

demonstrates that displays within the pair bond can evolve and persist if they cause a synergistic increase in investment by the display-receiving partner (male or female). However, it requires a preexisting bias to increase investment in the progeny as a response to displays. It is as if the pair needs a continual reminder that they have chosen to bond with a sexy partner.

Another paper by Servedio entitled, "The counterintuitive role of sexual selection in species maintenance and speciation", also scored high on my list of best talks. This one challenged the long-held view that sexual selection can drive and maintain species boundaries, especially in allopatric populations under secondary contact. Again using population genetic modelling, Servedio and Bürger surprisingly illustrate the inhibitory role that strong female preference plays in the maintenance of divergence. Even under scenarios that include strong selection against male traits that are locally maladaptive (independent of sexual selection), increasing female preference still breaks down divergence.

John Shorter

Michael Sheehan, winner of the Young Investigators' Jasper-Loftus Hill Award, presented a talk on "Individual recognition and the maintenance of phenotypic and genetic diversity". He first described a series of behavioral experiments demonstrating the variable facial color patterns used by *Polistes fuscatus* paper wasps as identity signals. Individual wasps benefit when they have rare, recognizable phenotypes and receive less aggression than wasps with common, indistinguishable appearances. The identity-signaling color patterns are heritable in *P. fuscatus*, suggesting that selection for distinctive appearances also maintains genetic variation. In humans, analyses of patterns of facial diversity with population genomic analyses of single nucleotide polymorphisms (SNPs) recently identified to influence normal facial morphology,

human facial identity may have evolved under negative frequency dependent selection, consistent with identity signaling. Face-associated SNPs tend of be old and of African origin, with some variants predating the split between the human and Neanderthal lineages.

Jessica Hayward gave a talk titled "Small dog, hairy dog, big dog, scary dog: understanding the genetics of morphological traits in the domestic dog". She investigates the genetic basis of body size and hair type. Genome wide association studies (GWAS) revealed additional novel loci, including a mutation in the gene MC5R that is associated with both the degree of fur shedding and medium versus short length fur. GWAS of individual and breed average body size measures yielded 17 key quantitative trait loci (QTLs), accounting for 80 to 85% of variation in weight and height. In contrast to humans, where many QTLs account for <40% of variation, a few QTLs of large effect account for most variation among dog breeds.

Simon Maddock talked about amphibians in the Seychelles. The Seychelles archipelago is unique among isolated island systems because of the occurrence of radiations of amphibians that have been separated from mainland relatives for at least 65 million years. The Seychelles species are unique in comprising the only island radiation of caecilians worldwide. Caecilians are considered intolerant to salt water, yet all but one Seychelles species occurs on more than one island, raising questions about within and among island variation. Simon analyzed external and cranial morphological data, and showed that variation is not similarly spatially structured in all species, and that differences do not wholly match predictions from ecology.

Olav Rueppell gave a talk on recombination in different honey bee species. *Apis mellifera*, the Western honey bee, has genome wide recombination of about 20cM/Mb. A recent linkage map in the closely related *A. cerana* has found similarly high recombination rates. Olav's group identified genome wide recombination maps of *A. florea* and *A. dorsata*, which had even higher recombination rates than previous species. So why would social insects have high recombination rates? Olav suggests that due to their life history, social insects live in very dense populations, and could be more susceptible to viruses, pests, and pathogens. A high recombination rate could lead to new genetic combinations, which may provide some resistance to quickly evolving diseases.

Genevieve Evans and Gunjan Arya

Steven Jones gave a wonderful presentation about snails, focusing on why snails have so much genetic variation and how temperature differences between habitats have an effect on not only color variation but

behavior as well. In addition to all that, he was able to present this information in a manner that would interest almost anyone by coupling his topics with art, which made this a fun talk to listen to. The variation of seminars offered gave the opportunity to experience talks from people most interested in narrowing the gap from lab research to field research, people interested in the active processes in hibernation and how they are regulated, to whole genome sequencing of Drosophila exposed to chronic malnutrition and its effect over 500 generations, including the observation of cannibalism. Of course, we cannot forget to mention talks about human diseases, including one about malaria that covered within-host competition through drug resistance and how this changes when you introduce a variety of strains and differences in the number of treated individuals. Overall, this was an enriching experience that broadens ideas in research and gives scientists and future scientists a chance to share and hear ideas to expand their work.

Lauren Dembeck

Mohamed Noor, President of the Society for the Study of Evolution, described his lab's work on the role of chromosomal inversions in maintaining species boundaries. In *Drosophila pseu*doobsura and *D. persimilis*, the inverted regions often show much higher genetic divergence than regions outside of the inversion suggesting a lack of recombination.

Keck Center alumna Amanda Moehring described a novel gene, *notu*, expressed in the brain that contributes to behavioral isolation between *Drosophila mauritiana* and *D. simulans*. *D. mauritiana* females refuse to mate with *D. simulans* males, while the reciprocal mating occurs readily. This is an important contribution to speciation research and helps to further elucidate the genetic basis of behavioral isolation.

The genus *Polyrhachis* consists of over 700 spiny ant species. Dirk Metzger showed evidence that their diversification likely started in South-East Asia using nuclear and mitochondrial genes.

Akihiko Yamamoto

The Dobzhansky prize winner Daniel Matute presented a nice story of a natural experiment of speciation at a small island off Africa between *Drosophila santomea* and *D. yakuba*. He described behavioral, zygotic and hybrid sterility between two species at the hybrid zone. He recapitulated the observed isolation mechanisms by laboratory experiments in just 10 generations. His research revealed development of isolation mechanisms through secondary contact of sister species.

Professional Development Workshop

Intersections of Genetics and Society

September 19, 2014

8:00 am - 12:30 pm Workshop in the Talley Center Coastal Ballroom

Featured speakers are Dr. George Church, Harvard University; Amy Harmon, The New York Times; Dr. Paul Lombardo, JD, Georgia State University; and Dr. Sarah Richardson, Harvard University.

The topics for discussion are

- 1) Wrestling with Interdisciplinarity and Highly Politicized Scientific Controversies
- 2) Facing the Potential for Human Genetic Engineering.

This workshop is open to graduate students and postdocs. Breakfast and lunch will be served.

REGISTRATION IS REQUIRED -- \$5 FEE.

Register at http://research.ncsu.edu/ges/events/current-future-events/prodevworkshop/

1:00 pm - 4:45pm Symposium in the Hunt Library Auditorium

- 1:00 pm 2:45 pm Dr. Paul Lombardo, Esq., Georgia State University: "Eugenics: Past and Future"
 - Dr. George Church, Harvard University: "The Future of Human Genomics and Synthetic Biology"
- 3:00 pm 4:45 pm Dr. Sarah Richardson, Harvard University: "How Culture Impacts Choices by Genetic Researchers"
 - Amy Harmon, The New York Times: "The Topsy-Turvy Debate Over Biotechnology in Agriculture"

The event is jointly sponsored by the Center for Genetics and Society, the Program in Genetics, the NCSU Libraries, the STS Center, and the W. M. Keck Center for Behavioral Biology

Voles and Fun in Oregon

by Caroline Leitschuh, Megan Serr and Andrea Vogel



Caroline Leitschuh, Megan Serr, and Andrea Vogel, along with Lisa McGraw, spent a weekend in July at the Oregon Health & Science University with about 50 other researchers to attend the Collaborative Biomedical Research Conference on the Vole Animal Model. The conference is intended to learn about the history of the vole as a research model, as well as current and future directions of the vole research community. Voles are small rodents that resemble stocky mice with shorter tails and while there are many species, the one with the biggest claim to fame is the prairie vole (Microtus ochrogaster). Prairie voles are a socially monogamous species, which is a unique trait for mammals. Many vole researchers, including McGraw and her lab, use the prairie vole as a model for human health and social interactions.

The conference focused on talks by leading researchers in the vole community with Dr. Sue Carter, formerly associated with UNC, being the keynote speaker. One of the first researchers to work on prairie voles, Carter summarized the noteworthy discoveries that have come from working with voles, including the roles of oxytocin

and vasopressin in partner bond formation, and in the bond between a mother and her offspring (in humans as well as voles). Other researchers spoke on topics as diverse as spatial use in monogamous species, the role of oxytocin in autism and depression, and how voles are used as a human model for studying sleep. McGraw spoke on current research in her laboratory at NC State, including individual variation in pair bonding. The McGraw laboratory is studying the strength of pair bonds in male voles, examining genetic components and heredity. Future research will involve asking the same questions about females.

The graduate students presented posters on their individual projects. Caroline will be using voles as a comparative model with wild mice, looking at the relationship between different types of housing and anxiety-like behavior. Megan is using voles to study female mate choice and assortative mating behaviors in wild mice and lab mice. Andrea is studying the role of seminal vesicle proteins in reproduction and pair bond formation. All three are grateful to have been able to attend the conference, and were inspired by the research presented.

Seminars

On **September 15**, 11:15 am, Dr. Michael R. Strand from the Department of Entomology at the University of Georgia (Athens, GA) will present a seminar titled "Viruses as mutualists: Life history evolution, genome architecture, and function."

The seminar will be in 3503 Thomas Hall. Refreshments will be served at 11:00 am.

On **September 25**, 3:30 pm, Dr. Ann-Shyn Chiang from the Brain Research Center, National Tsing Hua University, Taiwan and the Kavli Institute for Brain and Mind at the University of California at San Diego will present The Nina Allen Imaging Seminar, sponsored jointly by the Imaging Center and the W. M. Keck Center for Behavioral Biology, titled" Solving the fly brain."

The seminar will be in 101 David Clark Laboratories.

On **October 2**, 3:30 pm, Dr. Douglas J. Emlen from the Division of Biological Sciences at the University of Montana (Missoula, MT) will present a seminar titled "Mechanism(s) of extreme growth.

The seminar will be in 101 David Clark Laboratories.

On **October 2**, 7:00 pm, Dr. Emlen will present a public lecture at the North Carolina Museum of Natural Sciences in the Daily Planet Theater, Nature Research Center, 121 West Jones Street, Raleigh, NC 27601, titled "Extravagant weapons: A natural history."

On **October 6**, 1:30 pm, Dr. Marcus W. Feldman from the Department of Biology at Stanford University (Stanford, CA) will present a seminar titled "Some dynamics of cultural evolution."

The seminar will be in 3503 Thomas Hall.

Grants

Nadia Singh received a three-year \$619,708 grant from the National Science Foundation to study the genetic basis of phenotypic plasticity in meiotic recombination rate.

Reade Roberts received a four-year \$750,000 Beckman Young Investigator Award from the

Arnold and Mabel Beckman Foundation to develop a novel genetic model of dietary response and host-microbiota interactions.

Beth Dumont received a K99/R00 award from the National Institute for General Medical to study mechanisms of recurrent, parallel loss of X/Y pairing and recombination at meiosis in voles.

John Meitzen and Heather Patisaul received a Critical Issues in Clinical Research Pilot Project Grant from CCMTR/CVM as part of a multi-PI team to study early detection and neurological mechanisms of fescue toxicosis, a reproductive/growth disorder found in grazing cattle and horses.

Publications

The following publications from the W. M. Keck Center for Behavioral Biology have appeared in print:

Thresher, R. E., Hayes, K., Bax, N. J., Teem, J., Benfey, T. J. and Gould, F. (2014) Genetic control of invasive fish: technological options and its role in Integrated Pest Management. *Biological Inva*sions **16:** 1201-1216.

Shik, J. Z., Kay, A. and Silverman, J. (2014) Aphid honeydew provides a nutritionally balanced resource for incipient Argentine ant mutualists. *Animal Behaviour* **95:** 33-39.

Schmidt A. C., Dunaway L. E., Roberts J. G., McCarty G. S., and Sombers, L.A. (2014) Multiple scan rate voltammetry for selective quantification of real-time enkephalin dynamics. *Anal. Chem.* **86:** 7806-7812.

Huang, W., Massouras, A., Inoue, Y., Peiffer, J., Ràmia, M., Tarone, A. M., Turlapati, T., Zichner, T., Zhu, D., Lyman, R. F., Magwire, M. M., Blankenburg, K., Carbone, M. A., Chang, K., Ellis, L. L., Fernandez, S., Han, Y., Highnam, G., Hjelmen, C. E., Jack, J. R., Javaid, M., Jayaseelan, J., Kalra, D., Lee, S., Lewis, L., Munidasa, M., Ongeri, F., Patel, S., Perales, L., Perez, A., Pu, L., Rollmann, S. M, Ruth, R., Saada, N., Warner, C., Williams, A., Wu, Y-Q., Yamamoto, A., Zhang, Y., Zhu, Y., Anholt, R. R. H., Korbel, J. O., Mittelman, D., Muzny, D. M., Gibbs, R. A., Barbadilla, A., Johnston, J. S., Stone, E. A., Richards, S., Deplancke, B. and Mackay, T. F. C. (2014) Natural variation in genome architecture

among 205 *Drosophila melanogaster* Genetic Reference Panel lines. *Genome Res.* **24:**1193-1208.

Morozova, T. V., Mackay, T. F. C. and Anholt, R. R. H. (2014) Genetics and genomics of alcohol sensitivity. *Mol. Genet. Genomics* **289:** 253-269.

Mackay, T. F. C. and Moore, J. H. (2014) Why epistasis is important for tackling complex human disease genetics. *Genome Med.* **6:** 42.

Ellis, L. L., Huang, W., Quinn, A. M., Ahuja, A., Alfrejd, B., Gomez, F. E., Hjelmen, C. E., Moore, K. L., Mackay, T. F. C., Johnston, J. S. and Tarone, A. M. (2014) Intrapopulation genome size variation in *D. melanogaster* reflects life history variation and plasticity. *PLoS Genet.* **10:** e1004522.

Crissman, J. R., Booth, W., Santangelo, R. G., Mukha, D. V. and Schal, C. (2014) Hierarchical genetic analysis of German cockroach (*Blattella germanica*) populations from within buildings to across continents. *PLoS One* **9:** e102321.

Terrapon, N., Li, C., Robertson, H. M., Ji, L., Meng, X., Booth, W., Chen, Z., Childers, C. P., Glastad, K. M., Gokhale, K., Gowin, J., Gronenberg, W., Hermansen, R. A., Hu, H., Hunt, B. G., Huylmans, A. K., Khalil, S. M., Mitchell, R. D., Munoz-Torres, M. C., Mustard, J. A., Pan, H., Reese, J. T., Scharf, M. E., Sun, F., Vogel, H., Xiao, J., Yang, W., Yang, Z., Yang, Z., Zhou, J., Zhu, J., Brent, C. S., Elsik, C. G., Goodisman, M. A., Liberles, D. A., Roe, R. M., Vargo, E. L., Vilcinskas, A., Wang, J., Bornberg-Bauer, E., Korb, J., Zhang, G. and Liebig, J. (2014) Molecular traces of alternative social organization in a termite genome. *Nat. Commun.* 5: 3636.

Okamoto, K. W., Robert, M. A., Gould, F. and Lloyd, A. L. (2014) Feasible introgression of an anti-pathogen transgene into an urban mosquito population without using gene-drive. *PLoS. Negl. Trop. Dis.* **8:** e2827.

Li, F., Wantuch, H. A., Linger, R. J., Belikoff, E. J. and Scott, M. J. (2014) Transgenic sexing system for genetic control of the Australian sheep blow fly *Lucilia cuprina*. *Insect Biochem. Mol. Biol.* **51:** 80-88.

Bewick, S., Stuble, K. L., Lessard, J. P., Dunn R. R., Adler, F. R. and Sanders, N. J. (2014) Predicting future coexistence in a North American ant community. *Ecol. Evol.* **4:**1804-1819.

Terando, A. J., Costanza, J., Belyea, C., Dunn, R. R., McKerrow, A. and Collazo, J. A. (2014) The Southern megalopolis: using the past to predict the

future of urban sprawl in the Southeast U.S. *PLoS One* **9:** e102261.

Durham, M. F., Magwire, M. M., Stone, E. A. and Leips, J. (2014) Genome-wide analysis in Drosophila reveals age-specific effects of SNPs on fitness traits. *Nat. Commun.* **5**: 4338.

Stone, E. A. (2014) Predictor performance with stratified data and imbalanced classes. *Nat. Methods* **11:** 782-783.

Vensko, S. P. and Stone, E. A. (2014) No evidence for a global male-specific lethal complex-mediated dosage compensation contribution to the demasculinization of the *Drosophila melanogaster* X chromosome. *PLoS One* **9**: e103659.

Dolezal, A. L., Shu, X., OBrian, G. R., Nielsen, D. M., Woloshuk, C. P., Boston, R. S. and Payne, G. A. (2014) *Aspergillus flavus* infection induces transcriptional and physical changes in developing maize kernels, *Front. Microbiol.* **5:** 384.

Belcher, S. M., Cookman, C. J., Patisaul, H. B. and Stapleton, H. M. (2014) *In vitro* assessment of human nuclear hormone receptor activity and cytotoxicity of the flame retardant mixture FM 550 and its triarylphosphate and brominated components. *Toxicol. Lett.* **228:** 93-102.

Dale, A. G. and Frank, S. D. (2014) The effects of urban warming on herbivore abundance and street tree condition. *PLoS One* **9:** e102996.

Frank, S. D. (2014) Bad neighbors: urban habitats increase cankerworm damage to non-host understory plants. *Urban Ecosystems*: 1-11.

Of note...

Robert Anholt, Trudy Mackay, Genevieve Evans and Gunjan Arya attended the Evolution meeting in Raleigh.

Jen Baltzegar spent three weeks in Mexico completing a course entitled, "Pest Issues in Developing Nations: Biology, Culture, and Infrastructure."

Beth Dumont, Lauren Dembeck and John Shorter delivered talks at the Evolution meeting in Raleigh.

Fred Gould gave a presentation at the International Center for Maize and Wheat (CIMMYT) in Mexico, titled "Past, Present, and Future Genetic Engineering Technologies." He also spoke at the Gordon Research Conference on Science and Technology Policy on "Blending Sciences and Humanities Education at the Ph. D. Level." He has been selected to chair a new NAS-

NRC study on "Genetically Engineered Crops: Past Experiences and Future Prospects."

Caroline Leitschuh, Megan Serr, Andrea Vogel, Emily Moore and Kate Coyle presented posters at the Society for the Study of Evolution meeting in Raleigh, NC.

Lisa McGraw presented her work on voles at a symposium in honor of Dr. Mariana Wolfner's (her Ph. D. advisor) 60th birthday at Cornell University, Ithaca, NY. She also attended an NSF workshop on New Frontiers for the Integrative Study of Animal Behavior at the New York Genome Center. She presented a talk and students Caroline Leitschuh, Megan Serr and Andrea Vogel presented posters at the 2014 Vole meeting at Oregon Health Science University in Portland, OR.

John Meitzen serves on the program committee of the Research Triangle Chapter of the Society for Neuroscience, which has been re-activated. The first event will be held September 2, and will be a meet and greet with Representative David Price.

Mike Simone-Finstrom was an invited speaker at the International Society for Chemical Ecology meeting in Urbana-Champaign, IL., where he delivered a presentation on impacts of antimicrobial plant resins on honey bee gene expression. Together with **David Tarpy** he also co-authored a presentation titled "Unruly mates: no evidence for behavioral control or effort assessment in honey bee queen mating" at the International Society for Behavioral Ecology meeting in New York, NY.

Michael Simone-Finstrom and David Tarpy, D. gave a presentation on "Social context of disease resistance: Interactions among social and individual immune defense mechanisms in honey bees" at the Society for the Study of Evolution meeting in Raleigh, NC.

Nadia Singh and **Chad Hunter** attended the Society of Molecular Biology and Evolution conference in San Juan (PR) as well as the Evolution conference in Raleigh.

Samantha Smith was selected as an associate in the Society for Neuroscience Scholars Program, a competitive two-year program, sponsored by the National Institute of Neurological Disorders and Stroke that provides scientific and professional development opportunities for underrepresented neuroscience researchers.

Leslie Sombers was elected to the Board of Directors for the International Society for Monitoring Molecules in Neuroscience. She

presented an invited talk at the Monitoring Molecules in Neuroscience meeting, Los Angeles, CA, titled "Directly monitoring real-time enkephalin dynamics and modulatory effects using fast-scan cyclic voltammetry." Together with Lingjiao Qi, she also presented a talk titled "Ventral tegmental area mu-opioid receptor modulation of phasic dopamine release in the nucleus accumbens."

John Vandenbergh has served as a consultant to the Science Working Group at NASA to develop caging for sending male mice into space for experimental purposes. Males have not been previously used because of their aggressiveness but are needed for studies of male-related diseases.

To contribute to The Signal, to be placed on our mailing list or for information about the W. M. Keck Center for Behavioral Biology, contact Dr. Robert Anholt, Department of Biological Sciences, Box 7614, North Carolina State University, Raleigh, NC 27695-7614, tel. (919) 515-1173, anholt@ncsu.edu.

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