Peter and Rosemary Grant

Peter Grant is 'Class of 1877' Professor of Zoology and Professor of Ecology and Evolutionary Biology (Emeritus), Princeton University.

Rosemary Grant is Emeritus Professor, Senior Research Biologist, Ecology and Evolutionary Biology, Princeton University.

2005 Balzan Prize for Population Biology

Peter and Rosemary Grant are distinguished for their remarkable long-term studies demonstrating evolution in action in Galápagos finches. They have demonstrated how very rapid changes in body and beak size in response to changes in the food supply are driven by natural selection. They have also elucidated the mechanisms by which new species arise and how genetic diversity is maintained in natural populations. The work of the Grants has had a seminal influence in the fields of population biology, evolution and ecology.

Institutions Administering Research Funds:
Department of Ecology and Evolutionary Biology, Princeton University
Zoologisches Museum, Universität Zürich

Adviser for the Balzan General Prize Committee: John Krebs

Evolution in Small Populations

With their second half of the Balzan Prize, Peter and Rosemary Grant financed four lines of research concerned with mate choice and speciation in species of *Drosophila;* inbreeding and disease in small populations of Galápagos mockingbirds; the molecular basis of species-specific craniofacial patterning in birds; and beak development in an unusual Darwin's finch species, the warbler finch.

1. Mate choice and speciation in species of *Drosophila*. Margarita Ramos addressed the genetic bases and adaptive significance of morphological evolution in *Drosophila* by focusing on the pigmentation differences between *Drosophila yakuba* and *Drosophila santomea*. While *Drosophila yakuba* displays the typical abdominal pigmenta-

tion pattern of the *Drosophila melanogaster* subgroup, in *Drosophila santomea* both sexes have lost most pigmentation so that their abdomens appear yellow. *Drosophila santomea* is a species endemic to the island of São Tomé. Margarita developed and applied a technique for identifying the individual genes responsible for abdominal pigment differences between species. The laboratory research was supervised by Dr. David Stern at Princeton University.

2. Inbreeding and disease in small populations of Galápagos mockingbirds. With her study, Paquita Hoeck tested the hypothesis that reduced genetic variation due to inbreeding lowers the ability of small and inbred populations to respond to infectious diseases. For this purpose, four allopatric species of mockingbirds on the Galápagos Islands were studied, and the genetic variability in populations of different size was determined by using neutral genetic markers (microsatellites). The positive results are of direct importance to the conservation management of the endangered Floreana mockingbird species, which today consists of only 2 populations (20-45 individuals on Champion and approx. 100 on Gardner-by-Floreana). In collaboration with the Galápagos National Park Service and the Charles Darwin Research Station in Galápagos, it is planned to reintroduce this mockingbird species onto Floreana Island to re-establish a larger, third population that once existed on Floreana and became extinct due to human impact approximately 120 years ago. This research was supervised by Dr. Lukas Keller at Universität Zürich.

3. The molecular basis of species-specific craniofacial patterning in birds. Céline Clabaut (post-doctoral fellow) studied the molecular basis of craniofacial patterning in Darwin's medium ground finches of the Galápagos under the direction of Dr. Arkhat Abzhanov at Harvard University. Dr. Abzhanov had already found that the level and timing of expression of Bone Morphogenetic Protein 4 (Bmp4) in the distal mesenchyme of the upper beak is correlated with wider and deeper beaks. The main aim of Céline Clabaut's Balzan Foundation fellowship was to study the genetic basis of species-specific Bmp4 expression. Together, they were able to (1) show that the Bmp4 coding sequence in Darwin's Finches is too conserved to be responsible for the species specific expression of Bmp4; (2) start the analysis of cis-regulatory changes; and (3) develop two powerful approaches to identify the enhancers: first, long-range detection of the enhancer activity with transgenic hybrid mice, and second, a more precise search using a lentivirus approach.

4. Beak development in an unusual Darwin's finch species, the warbler finch. Jennifer Gee (post-doctoral fellow) worked in the same lab as Céline, applying similar techniques to the investigation of differences between the warbler finch (*Certhidea*) and the ground finches (*Geospiza*). Results from this study suggest that the unique pointed and elongate shape of the warbler finch beak results from suppression of the same molecular factors that are upregulated in the ground finches with broad and wide bills. Thus, the ancestor of the warbler finch may have had a more typical Darwin's finch bill and a developmental program corresponding to this morphology. The candidate gene approach was used to detect differences at early stages of development, and as in Clabaut's project, chicken material is being used to try out new techniques before chosen ones are applied to the limited finch material.

A two-day Balzan Symposium *Population Biology and Evolution,* dedicated to the overall results was held on 5 and 6 September 2008 at Princeton University. Participants were: Michael Arnold (University of Georgia), Leticia Avilés (University of British Columbia), Veronica Barragán (Universidad San Francisco de Quito, Ecuador), Kimberly Bostwick (Cornell University), Paul Brakefield (University of Sheffield), Jeffrey Feder (University of Notre Dame), Michaela Hau (Universität Konstanz), Raymond Huey (University of Washington), Richard Lenski (Michigan State University), Jonathan Losos (Harvard University), H. Frederik Nijhout (Duke University), Mohamed Noor (Duke University), Stephen Nowicki (Duke University), Nicolás Peñafiel (Universidad San Francisco de Quito, Ecuador), Kenneth Petren (University of Cincinnati), Paolo Piedrahita (La Pontificia Universidad Católica del Ecuador), Uli Reyer (Universität Zürich), Robert Ricklefs (University of Missouri St Louis), Michael Ryan (University of Texas), Pablo Sanchez (La Pontificia Universidad Católica del Ecuador), Kerry Shaw (Cornell University), Thomas Smith (University of California, Los Angeles), Klaus Schwenk (Goethe-Universität, Frankfurt am Main), John Thompson (University of California, Santa Cruz), David Wake (University of California, Berkeley), Mary Jane West-Eberhard (Smithsonian Tropical Research Institute), Martin Wikelski (Max-Planck-Institut für Ornithologie).

Researchers:
Céline Clabaut
Jennifer Gee
Paquita Hoeck
Margarita Ramos-Womack

Publications:

Hoeck PEA, Beaumont MA, James KE, Grant BR, Grant PR, Keller LF. 2010. Saving Darwin's muse: evolutionary genetics for the recovery of the Floreana mockingbird. Biology Letters. 6: 212-215.

Hoeck PEA, Bollmer JL, Parker PG, Keller LF. 2010. Differentiation with drift: a spatio-temporal analysis of Galapagos mockingbird populations (Mimus spp.) Philosophical Transactions of the Royal Society B. 365: 1127-1138.

Rebeiz M, Ramos-Womack M, Jeong S, Andolfatto P, Werner T, True J, Stern D, Carroll S. 2010. Evolution of the tan Locus Contributed to Pigment Loss in *Drosophila santomea*: A Response to Matute et al. Cell. 139, (6): 1189-1196.

Grant PR, Grant BR. 2008. How and Why Species Multiply. The Radiation of Darwin's Finches. Princeton (NJ): Princeton University Press.

Grant PR, Grant BR., eds. 2010. In Search of the Causes of Evolution. From Field Observations to Mechanisms. Princeton (NJ): Princeton University Press.

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