Peter and Rosemary Grant

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.

Evolution in Small Populations

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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. A two-day symposium dedicated to the overall results was held on 5-6 September 2008 at Princeton University.

1. *Mate choice and speciation in species of* Drosophila. Margarita Womack Ramos has 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 pigmentation 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 has been 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 inbreed-

ing lowers the ability of small and inbred populations to respond to infectious diseases. To this aim, four allopatric species of mockingbirds on the Galápagos Islands were studied and the genetic variability in populations of different size is determined 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 has been supervised by Dr. Lukas Keller at the University of Zurich.

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) has 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 is being used to detect differences at early stages of development; and as Clabaut's project, chicken material is being used to try out new techniques before chosen ones are applied to the limited finch material.

Participants to the Balzan Symposium on "Evolution in Small Populations": Michael Arnold (University of Georgia), Leticia Avilés (University of British Columbia), Veronica Barragán (University of San Francisco, Quito, Ecuador), Kimberly Bostwick (Cornell University), Paul Brakefield (University of Sheffield), Jeffrey Feder (University of Notre Dame), Michaela Hau (University of 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 (University of San Francisco, Ouito, Ecuador), Kenneth Petren (University of Cincinnati), Paolo Piedrahita (Catholic University of Ouito, Ecuador), Uli Rever (University of Zurich), Robert Ricklefs (University of Missouri St Louis), Michael Ryan (University of Texas), Pablo Sanchez (Catholic University of Quito, Ecuador), Kerry Shaw (Cornell University), Thomas Smith (University of California Los Angeles), Klaus Schwenk (Goethe University Frankfurt), 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 Institute for Ornithology, Migration and Immuno-ecology).

Publications:

- Hoeck, P. E. A., Beaumont, M. A., James, K. E., Grant, B. R., Grant, P. R. and Keller, L. F., *Saving Darwin's muse: evolutionary genetics for the recovery of the Floreana mock-ingbird*, "Biology Letters", 6: 212-215, 2010.

- Hoeck, P. E. A., Bollmer, J. L., Parker, P. G. and Keller, L. F., *Differentiation with drift: a spatio-temporal analysis of Galapagos mockingbird populations (Mimus spp.)*, "Philosophical Transactions of the Royal Society B", 365: 1127-1138, 2010.

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

Statements by the Prizewinners:

Being chosen for an award by the internationally renowned Balzan Foundation is an extreme honour, and something very, very special. It is special because, alone among the Foundations which I know, the Balzan Foundation makes funds available to young investigators in the field of the recipient. Peter Grant (Berne, 11.11.2005)

I am grateful to the Balzan Foundation for recognizing and celebrating the value of scholarship, and deeply grateful for the wonderful opportunity this Prize gives to young research scholars of the future. It is foundations, such as the Balzan Foundation, with its wisdom *in fostering inter-cultural and inter-generational exchange that will, surely, make tomorrow's world a better and a more humane place.* Rosemary Grant (Berne, 11.11.2005)

With prize money received from the Foundation we have supported the research of four young investigators over a period of three years. The research of the two post-doctoral fellows has been completed. Research of the two graduates approaches completion, and all research funds have been spent. Publications are planned, and in all cases the research is continuing with funds from other sources. At the conclusion of the supported research of the two post-doctoral fellows we organized a conference, entitled Evolution in Small Populations, to give the young investigators the opportunity to present their results to an invited audience of approximately 100 scientists with similar research interests. The conference was held at Princeton University on September 5th and 6th. It consisted of 32 presentations. Twenty-four were lectures given by established scientists in ecology, behavior and evolution, coming from Costa Rica, Britain, Switzerland and Germany as well as the U.S. and Canada. Four more were lectures given by the young investigators, and another four were short summaries of research given by recent graduates from Ecuadorian Universities, supplementing their poster presentations. We invited the Ecuadorian students to attend as a means of transmitting some of the benefits we have reaped from our research back to the country that has helped us. We believe the conference was an outstanding success, both in the lecture hall and outside during coffee breaks and meals when students and senior research workers were able to interact in small groups and establish valuable professional contacts as well as friendships. Peter and Rosemary Grant (December 2008)

Five years ago we were the fortunate recipients of the Balzan Prize for our research findings, and we have devoted half the prize money to the support of four young investigators in research that is related to our own interests. In the first half of this lecture, I will outline their findings. Peter Grant (Accademia Nazionale dei Lincei, Rome, 13.5.2010)

So, I'd like to leave you with one message, and that is a conservation message: what our work has shown is that neither species nor environment are static entities, but they are dynamic and constantly changing, and to conserve species and the environment we must keep them both capable of further change. And I would like to thank the Balzan Foundation for supporting four wonderful young scientists, and their studies linking genetics, behavior and ecology with evolution, which have really supplemented ours. They have greatly contributed to a much more mechanistic understanding of the diversity of life. Thank you. Rosemary Grant (Accademia Nazionale dei Lincei, Rome, 13.5.2010)