



International Balzan Foundation

# Peter and Rosemary Grant

2005 Balzan Prize  
for Population Biology

Excerpt from the book  
*Premi Balzan 2005. Laudationes, discorsi, saggi*, Milan, 2006  
(revised and enlarged edition, 2010)

*This monograph on Peter and Rosemary Grant  
has been re-published on the occasion  
of the two hundredth anniversary  
of the birth of Charles Darwin.*

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## 2005 Balzan Prize for Population Biology

### Motivation for the Prize and *laudatio*

**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.**

The 14 species of finches that inhabit the Galápagos Islands were amongst the key inspirations for Charles Darwin in his elucidation of the now universally accepted mechanism of evolutionary change: natural selection. On his journey on the HMS Beagle, Darwin visited the Galápagos archipelago and he inferred that the species of finches he observed had affinities with species on the mainland of South America. He hypothesised that the different species with different beaks had arisen through adaptation to local ecological conditions on different islands as a result of natural selection. Evidence from other species suggested that geographical separation of each island population was an important requirement for their divergence. This process of evolutionary change in the formation of new species became the central thesis of Darwin's 1859 book *On the Origin of Species*.

The Grants have brought Darwin's work into the 21st century, by an extraordinary long-term study that has combined the tools and intellectual frameworks of ecology, behaviour, genetics and evolution. Their findings have essentially confirmed and expanded Darwin's hypothesis, but have placed it in a contemporary idiom by analysing the underlying mechanisms.

First, they have shown how rapid the action of natural selection can be. They discovered that when the food supply of the birds changes from year to year, as a result of climatic variation from El Niño events, there is intense natural selection resulting in changes in beak size and shape as well as body size. In years when

the seeds are harder, birds with bigger, stronger beaks are at a selective advantage and in other years, the opposite is true. Two remarkable aspects of this finding are: a) the amount of genetic variation for these ecologically important traits (beak and body shape) in natural populations is substantial, and b) features of these populations can change very rapidly. Both of these discoveries were a major surprise to evolutionary biologists at the time.

Second, the Grants have shown the mechanism by which different populations of the Galápagos finch may become reproductively isolated, and hence eventually evolve into new species. They discovered that, in choosing a mate, female Galápagos finches discriminate between males on the basis of their songs. Both the song itself and the preference for a particular song are passed from parent to offspring through learning. Songs are culturally transmitted from father to son. This process ensures that females mate only with males of similar background, hence establishing reproductive isolation between groups, an essential ingredient of speciation. Reproductive isolation between Galápagos finch species is not, however, complete. Occasionally hybrids are produced and these are sometimes, but not always, at a selective disadvantage. When successful they help transfer genes among species, thus maintaining if not increasing genetic diversity among populations.

Third, the Grants have used variation in mitochondrial DNA and microsatellite regions of nuclear DNA to show that the 14 species of finch have indeed evolved from a common ancestor that arrived in the Galápagos 2-3 million years ago. They have also been able to identify a gene, *Bmp4*, which influences the development of beak shape and therefore could have played an important role in the evolutionary divergence of the Galápagos finches.

The Grants' work on Galápagos finches is universally recognised as perhaps the most significant field study of evolution in action of recent decades. It is cited in all the major textbooks on evolution and has been the subject of a popular science book *The Beak of the Finch: A Story of Evolution in Our Time* by Jonathan Weiner (1994, Alfred Knopf, New York).

The Grants are outstanding scientists in their field and worthy recipients of the Balzan Prize for Population Biology.

**Prizewinners' acceptance speeches**

National Council Hall, Berne – 11 November 2005

*Federal Councillor,  
Presidents of the Balzan Foundation,  
Members of the Foundation,  
Ladies and Gentlemen,*

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. This is particularly appropriate in our case. Our research over the last 33 years has centered on a related set of questions in one place, the Galápagos archipelago, and may be likened to an edifice built on volcanic rock. Seven young scholars helped us build the foundations: three post-doctoral fellows and four graduate students. Now, three decades after they helped us build our foundation, the Balzan Foundation enables us to help another generation of young scholars build theirs.

The second reason for being delighted to receive this prize is that it is an affirmation of the research we have chosen to conduct in the fields of population biology and evolution. Rather than tread a beaten path we have blended the ecological discipline of field biology with methods of genetics to reveal the power and frequency of natural selection as a cause of evolution; and have done so in the same environment that inspired the young Charles Darwin. Darwin believed that evolution would be manifest only with the passage of vast amounts of time. Now it is apparent that evolution happens in our lifetime, and sometimes very fast.

The third and most personal reason to be so gratified at sharing the prize with Rosemary is that it endorses the possibility of a husband and wife working together, equally, as a team, without regard to individual advancement and recognition. In receiving the prize jointly we hope this will be an encouragement to other couples who might wonder whether they will be able to conduct scientific research in tandem rather than solo.

Conscious of the list of distinguished scholars who have been similarly recognized I accept my share of the award of the Balzan Prize in population biology for the year 2005, with great pleasure, gratitude and humility.

*Peter R. Grant*

*Federal Councillor,  
Presidents of the Balzan Foundation,  
Members of the Balzan Foundation,  
Ladies and Gentlemen,*

To be the recipient of the 2005 Balzan Prize for Population Biology is a great honor and one for which we are profoundly grateful. It is also a great personal pleasure to receive this award in Switzerland, because the stimulating months we spent at the University of Zürich meant much to us, and left us with many fond memories and enduring insights.

It is a particular privilege to receive this honor from a Foundation whose aim is “to foster on a world-wide level, culture and science, outstanding humanitarian causes, and peace and brotherhood among people regardless of nationality, race or creed”.

These are noble aims and ones that resonate with us because one of the most persistent lessons we have learned through our collaborations with scholars in many countries is that inter-cultural communication, whether between people from different ethnic backgrounds or between people from different scientific disciplines, bring with it a tremendous depth of understanding, respect and wisdom.

While it is often said that we cannot choose our parents or ethnicity, we can choose our friends, and a common interest can overcome barriers of race, religion, age and socioeconomic status. The rewards of an interchange of ideas and information between cultures are immense, much about the systems of inequality that plague us today are revealed, and we see more clearly the strengths and

imperfections of our own and other cultures. Therein lies our hope for imaginative and ingenious solutions to the problems of today.

In our own research, collaboration with colleagues from a multitude of disciplines has worked synergistically and led to a fuller understanding of both the problem and the solution. By taking a multifaceted approach and using information from the fields of genetics, developmental biology, paleontology, behavior and ecology we have collectively been led to exciting discoveries, which are contributing to a more mechanistic understanding of how evolution has produced the diversity of organisms we see in the fossil record and in the world around us today.

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.

*B. Rosemary Grant*

## Population Biology and Speciation\*

by Peter R. Grant

Class of 1877 Professor of Zoology, Princeton University, Princeton, New Jersey  
and B. Rosemary Grant

Research Scholar and Professor, Princeton University, Princeton, New Jersey

A fundamental problem in biology is to understand the steps involved in the process of speciation, because the question of how one species splits into two addresses the foundation of the biodiversity we see around us in the world today.

Beginning in 1973 we chose to address this problem with a study of Darwin's finches in the Galápagos archipelago. This young adaptive radiation in an isolated archipelago is a particularly suitable system for asking questions about adaptation and the multiplication of species: how these processes happen, and how to interpret them. The unique advantages are that all 14 species of Darwin's finches are closely related, having been derived from a common ancestor in the last 2-3 million years. None of the species has become extinct as a result of human activity, thereby creating missing links. They live in the largely undisturbed environment in which they evolved, they are distributed in various combinations across islands, and they exhibit various degrees of morphological distinctness. Thus, considering populations across the entire archipelago, it is as though the whole process of speciation in all of its stages from the initial colonization through divergence to the formation of a reproductive barrier between species has been frozen in space, allowing us to investigate each step in turn.

### Background

Three inter-related problems preoccupied us from the outset: how is speciation to be explained; how, and how often, does adaptation to the ecological environment occur; and how is quantitative genetic variation in small populations maintained in the face of depleting forces of natural selection and random genetic drift. To address these problems we developed the strategy of combining archipelago-wide comparative studies of different combinations of finch species with intensive long-term studies of population processes on the islands of Genovesa (11

\* Paper published in the book *Premi Balzan 2005. Laudationes, discorsi, saggi*, Milan, 2006.

years) and Daphne Major (33 years). By simultaneously taking account of ecological, behavioral and genetical aspects of evolution, and being alert to their interconnectedness, we hoped to reach a greater understanding of finch evolution than would be possible from a narrower focus on just one of them.

### **Speciation**

Speciation begins when a new population is established, continues with the divergence of that population from its parent population, and is completed when members of two diverged populations coexist in the same place without interbreeding. The question is how do these processes occur? We stand a virtually negligible chance of observing the whole process under natural conditions. Nevertheless it is possible to make relevant observations in nature of all steps in the process.

The first step involves ecological divergence. One way this happens is through the fundamental evolutionary process of adaptation to the environment through natural selection of heritable phenotypic variation. Usually adaptation is inferred, rarely is it studied directly. Our studies have been able to accomplish both.

### **Adaptation Inferred**

Adaptation of finches on different islands had previously been inferred from the association between beak size and shape of several species on the one hand and characteristics of the diet on the other (Lack, D., *Darwin's Finches*, Cambridge University Press, Cambridge, 1947). Our initial studies strengthened the inference through sampling, measurement and quantification of the physical characteristics of foods available in the environment on several islands, the foods actually eaten, and beak dimensions.

Earlier, David Lack had two important insights into the adaptive evolutionary history of the finches. These were a) competitive interactions between species explain some mutually exclusive distribution patterns and enhanced beak size differences between sympatric finches (character displacement), and b) competitive interactions are expected to be most severe in the dry season when food is likely to be in short supply. Both were supported by our fieldwork. A modeling exercise produced a better fit between observed and predicted beak sizes when competitive interactions were incorporated than when they were not. Dry season food supplies are indeed lower than wet season supplies, with few exceptions, and as

food supply declines so do population sizes. Thus species adapt to the environment, and an important part of the environment is the presence of competitor species. Both of Lack's insights were valuable and correct.

### **Natural Selection Observed**

Inferences about adaptive evolution in the past are more plausible if supported by a demonstration of evolution in the present. We gained insights into adaptation through long-term studies of ground finch (*Geospiza*) populations on both Genovesa and Daphne Major. By capturing and measuring a large number of finches and marking them with unique combinations of colored leg bands we were able to follow their fates. This simple and well-used technique of population study revealed the tempo of ecological and evolutionary change. It showed that ground finches can live as long as 16 years, which was a surprise given the occasionally harsh climatic environment of lowland Galápagos habitats, and shorter maximum lives of north temperate relatives. More remarkable was the discovery that significant adaptive change takes place in less than a year, and is therefore, potentially at least, a rapid process and not an immeasurably slow one as was believed at that time.

Natural selection was clearly demonstrated during the drought on Daphne Major Island in 1977. Medium ground finches (*Geospiza fortis*) consumed a large fraction of the supply of small seeds, and then turned increasingly towards the large and hard seeds, now in relatively high abundance. Only large finches with large beaks could crack the seeds and extract the kernels, hence they survived at a relatively high frequency. Natural selection had occurred. Over the 33 years we discovered that natural selection is not restricted to one trait, one species or one island; it also occurred in the population of cactus finches (*Geospiza scandens*) on Daphne, and in *G. conirostris* (large cactus finch) and *G. magnirostris* (large ground finch) on Genovesa. Natural selection occurs frequently, and varies in direction and strength according to the particular set of environmental conditions.

For natural selection to cause evolution the trait in question must be heritable. We were able to show that the morphological traits subject to natural selection (beak and body size) were highly heritable, and that genetic correlations among them were generally very strong and uniformly positive. These results were used to predict evolutionary responses to repeated natural selection, and predictions were then compared to actual changes from generation to generation. Matches between observa-

tions and predictions were close, both after the 1977 drought and following selection events in later years, thus demonstrating that natural selection drives frequent evolutionary changes in nature. This provides an important insight into the evolutionary lability of populations when subjected to environmental change. For example it helps to make sense of large changes in several organisms occurring in an apparently short period of time in the paleontological record.

An additional insight was the realization that continuous monitoring of the environment is as important for an understanding of long-term evolution as is the continuous monitoring of the finch populations themselves. This insight emerged from a study of the effects of the El Niño event of 1983. Unprecedented in the century in length and severity, it was followed two years later by a drought. The contrast could scarcely have been more extreme. A simple expectation would have been that the selection event of 1977 would be repeated in 1985. That expectation would have been entirely wrong, because the vegetation and hence food environment had changed profoundly during 1983, from dominance of large-seed producing plants to dominance of small-seed producing ones. This change lasted for a long time. Small seeds continued to be abundant in the seed bank until 1999. In the most recent six, relatively dry, years the vegetation has changed both in composition and quantity back towards the pre-1983 condition, but has not reached it yet.

The important point is that no two droughts have the same effects; the particulars depend on initial conditions. Droughts have selective or non-selective effects on the finches depending on whether large seeds or small ones (and which ones) are plentiful at the start of a drought, as well as on the preceding evolutionary history of the finches. The drought of 1977 had strong selective effects on the beak traits of two species of finches, the 1985-86 drought had weaker effects in an opposite direction on beak traits of one of the species, and the drought of 1988-89 had no selective effects on either.

The study provides an empirical foundation for general theories concerning adaptation to food resources with or without the diversification of species. Additionally it has yielded the surprising fact that as a result of natural selection the finches on Daphne Major Island are not morphologically or genetically the same as their ancestors were 30 years ago. Their environment has changed, and so have

they. In collaboration with colleagues at Harvard University, Arkhat Abzhanov and Cliff Tabin, we are currently exploring evolutionary change of beak dimensions at the molecular genetic level.

### **Colonization and Founder Effects**

The classical founder effect model of speciation of Ernst Mayr proposes that the crucial step in speciation occurs right at the beginning of the founding of a new population by a few individuals. Rapid evolution could occur as a result of inbreeding, random genetic drift, the loss of genetic variation, and selection of sets of genes whose interactions change as a result of substantially altered allele frequencies. If the changes are profound enough they may yield a new species, reproductively isolated from the population that gave rise to it when they later come into contact. Although much has been written about possible evolutionary consequences of founder events, there have been very few opportunities to examine the genetic changes that actually occur in nature. We were fortunate to witness the founding of a new population on Daphne Major Island, and were thus able to make a direct assessment of this model. Two female and three male large ground finches *Geospiza magnirostris* established a breeding population at the end of 1982 when a major El Niño event had just got underway. We followed their fates and the fates of their descendants for the next 20 years.

As expected from the founder effects model inbreeding depression occurred in the first 10 years, and was actually more severe than ever recorded in the two resident populations of *G. fortis* and *G. scandens*. However survival of the first inbred individuals was unexpectedly high. Often more can be learned from exceptions like this than from observations that agree with expectations. The insight gained from this surprising observation was that genetic disadvantages from inbreeding can be over-ridden by the ecological advantages of abundant food and the absence of density dependent effects on survival. Another unexpected observation was recurrent immigration, from more than one island source and not just from the island closest to Daphne. Recurrent immigration contributed to the elimination of any long-lasting effects of inbreeding, and to the fact that no substantial change in either phenotypic traits or in microsatellite allele frequencies occurred. Insofar as the observations can be generalized they provide no support for the model of founder effect speciation, and showed how it can fail. Yet even if this specific model is not applicable, speciation may nonetheless be more likely to proceed in small insular populations than in large ones, as discussed below.

### **Byproduct of Adaptation**

An alternative to speciation through founder effects is Theodosius Dobzhansky's adaptive byproduct hypothesis of speciation. If the same morphological traits that undergo adaptive change also function in a reproductive context when individuals choose mates then speciation might proceed as a simple consequence of the adaptive change. No special genetic factors need be invoked to explain the splitting of ancestral populations into separate species, since ecological factors are the primary driving force of differentiation according to this explanation, and the avoidance of interbreeding (pre mating isolation) when they later come into contact with each other is a passive, secondary, consequence of the adaptive change.

Our early studies on Daphne, Genovesa and several other islands showed the importance of ecological factors, mainly the composition of the food supply, which varies from island to island. With this in mind it is easy to see how finches that dispersed from one island and established a new breeding population on another would encounter a different constellation of foods, and undergo evolutionary adaptation in beak traits to the new food supply. By itself this would raise barriers to gene exchange between the original and the derived populations if beak size and shape were also the key traits used by finches in choosing a mate, and if adaptive divergence was large. Discrimination experiments with stuffed museum specimens of birds supported the hypothesis. Responding birds of different ground finch species tested on Daphne, Genovesa and other islands discriminated between local members of their own species and either a resident, closely-related, species or different conspecifics from another island. They did so on the basis of beak size and shape differences. Two other possibilities can be ruled out; body sizes were the same in some of the tested pairs and plumages were identical in all of them.

One awkward fact does not fit the byproduct hypothesis: on Daphne and elsewhere the largest members of a small species (e.g. *G. fuliginosa*) are more similar in beak size to the smallest members of a larger species (*G. fortis*) than they are to most members of their own population. If beak traits are the only factor in mate choice the species should hybridize, and those individuals that do so should be similar in beak size. Long-term studies were needed to establish the fact that some species of Darwin's finches do indeed interbreed, though rarely, all previous evidence of hybridization being ambiguous. Gene exchange between species was confirmed by identifying the parents with microsatellite DNA. The study on Daphne yielded the

unexpected result that when *G. fortis* and *G. fuliginosa* hybridize they do so without apparent regard to their respective beak sizes. This does not contradict the byproduct hypothesis but shows it is insufficient. Something else is involved in mate choice that usually leads to conspecific pairing but occasionally gives rise to hybridization.

That something else is song. The initial argument for the importance of song was developed by Robert Bowman, with rich support from analyses of song and sound transmission profiles. He showed that some features of song (pitch) varied among species as a function of their body size, and others varied as a function of the sound transmitting properties of the habitats they occupied. We later demonstrated with song playback experiments, in the absence of any morphological cues, that individuals could discriminate between their own species song and the song of related species. Thus two sets of experiments show that song and beak morphology are used as cues in mate choice. Why, then, do species sometimes hybridize? The answer lies partly in how finches acquire their songs and other information that they use later in choosing a mate.

A small number of laboratory experiments, conducted by Bowman, with finches exposed to tape-recorded song early in life showed that songs are learned between the ages of 10 and approximately 30 days after hatching by an imprintinglike process. Only one song is sung, by males and not females, and once learned it remains constant for life. These results combined with pedigree analyses on both Daphne and Genovesa demonstrated that song is typically transmitted from father to son. Nevertheless, the normal cultural transmission process can be perturbed by the misimprinting of young birds on the song of another species. Insights into the causes of perturbations have been gleaned over a very long time on Daphne, with difficulty because it is rare and because the circumstances are idiosyncratic. For example in one case an aggressive pair of *G. scandens* displaced the *G. fortis* owners of a nest and raised the offspring that hatched from one *G. fortis* egg together with their own offspring. The fostered *G. fortis* male later sang a *G. scandens* song.

A key insight into how song and beak traits are used in mate choice emerged from the pedigrees: paternal song is the primary cue for both males and females in hybridizing and backcrossing pairs. Misimprinted birds mate according to song type rather than morphology. The hybrid offspring breed with members of the species that sing the same song type as their fathers. Beak traits become the primary cue on-

ly when there is a large difference in beak size between the hybrid or backcross individual and the potential mates of the species that sing its song. For example, *G. fortis* individuals that have misimprinted on the song of the much larger *G. magnirostris* on Daphne have not hybridized. A parsimonious explanation for the development of mate preferences is that song is learned from parents and other conspecific individuals in association with morphological traits, primarily beak size and shape.

### **A Model of Adaptation and Chance**

Speciation begins in allopatry as a result of local adaptation in genetically transmitted beak traits that also function in mate choice. Culturally transmitted song traits also diverge. Some song features such as frequency vary in relation to body size, and others, such as note repetition rate, vary in relation to beak size and jaw musculature possibly independent of body size. Thus several facts about Darwin's finches are consistent with the adaptive by-product hypothesis of Dobzhansky. Yet there are two reasons for thinking that a more comprehensive model of speciation is needed.

First, there is a need to make explicit the role of learning in the development of mate preferences; mate preferences are not inherent or "genetically fixed". One consequence of learning is that species can sing each other's songs, within limits, despite beak shape differences, and base their choice of mates largely upon learned song. Thus a crucial question is just what features of song are used in mate choice, and how do these diverge? Whatever causes songs to diverge in allopatry promotes speciation.

Second, there is a need to explicitly incorporate the role of chance because it is an important factor in song divergence. Change in the composition of individual songs from one generation to the next probably occurs through copying errors, as we have seen manifested on Daphne in minor ways. The most egregious example was an unusual song variant in the *G. scandens* population apparently caused by a cactus spine in its throat! Its sons learned and sang the same strange song, and at least two generations later there were five males on the island singing this song. Frequencies of song variants are subject to random change across generations due to some males leaving more sons than others, much as the frequencies of selectively neutral alleles drift at random. We have documented this on Daphne, in both *G. fortis* and *G. scandens* populations, as well as in the *G. magnirostris* population in the first few years following colonization of the island.

The importance of chance in speciation is underlined by the fact that populations of the same species on adjacent islands with nearly identical habitats may sing different songs. The strongest example is the sharp-beaked ground finch, *Geospiza difficilis*, on the northern islands of Wolf and Darwin. There are no habitat or morphological differences between the populations that would help to explain the differences in song, and we are left with randomness in the colonization of the two islands, or random cultural drift in song characteristics akin to random genetic drift, as explanations. Playback experiments on one or both islands are needed to test if the birds on one island would respond to songs from the other. The differences are so large, it seems highly likely they would ignore each other, because *G. difficilis* individuals on a third island, Genovesa, do distinguish between songs from Wolf and their own, similar, songs. In this case subtle, not profound, differences between Genovesa and Wolf songs, probably in temporal patterning, set up a potential reproductive barrier between the two populations.

#### **Time-dependent Molecular Change**

Another possibility is that populations stay isolated on different islands long enough for reproductive barriers to arise simply as a result of the accumulation of different alleles through mutation. Then, at the extreme, when members of the two populations encounter each other they are unable to produce viable and fertile offspring, even if they choose to mate with each other, because the species are genetically incompatible: during development of the offspring adverse interactions occur between the maternal and paternal genomes.

Genetic incompatibilities have not been detected between any of the four hybridizing pairs of ground finch species on Daphne and Genovesa. This statement applies to both survival and reproductive aspects of hybrid and backcross fitness. In following the fates of hybrids and backcrosses to determine where they might be at an expected disadvantage in relation to the parental species we gained the important insight that their fitness is not fixed but is environment-dependent: just as environmental variation alters the fitness of inbred birds so does it influence the fitness of hybrids and backcrosses.

From 1973 to 1982 the few hybrids that were produced by *G. fortis* breeding with either *G. fuliginosa* or *G. scandens* on Daphne did not survive to breed (nor did many of the non-hybrids). At this time we thought they survived poorly because

of genetic incompatibilities. The successful breeding of hybrids and backcrosses from 1983 onwards showed this was wrong. Instead their fates were governed by the food supply. Before 1983 the large, hard *Opuntia echios* seeds and woody *Tribulus cistoides* fruits dominated the food supply. Hybrids were unable to crack open *Tribulus* fruits to reach the seeds and took twice as long to open *Opuntia* seeds as *G. scandens*. The switch to an abundant and continued production of small soft seeds after the 1983 El Niño produced a food supply appropriate for hybrids and backcrosses with their intermediate beak sizes. Since 1983 the survival of hybrids and backcrosses has been equal to or even greater than survival of the pure species.

These findings show that in the course of speciation learned behavior is of paramount importance in the establishment of a barrier to interbreeding. Only later do the species accumulate so much genetic change that they are incapable of forming viable and fertile offspring through interbreeding should they attempt to do so. This later point marks the unquestionable completion of speciation. Many if not all coexisting populations of Darwin's finches have not yet reached this point, although they function as species by remaining distinct even in the face of occasional gene exchange.

### **Maintaining the Potential for Evolutionary Change**

In the last million years or more oscillations between glacial and inter-glacial conditions at temperate latitudes have caused sea level to rise and fall. Small islands have been repeatedly created and submerged in the Galápagos archipelago. Their populations of finches could have been the starting point for species formation through selection and hybridization. Contemporary study of finch populations on a small island such as Daphne can throw light on these dynamics, and in particular on the question of how quantitative genetic variation is maintained.

Genetic variation is lost through drift and selection and regenerated by mutation. In principle rates of losses and gains could be equal, yielding an equilibrium level of genetic variation maintained for a long time. At the outset this simple scheme seemed insufficient to explain the high levels of phenotypic and presumed genetic variation in quantitative traits in many Darwin's finch populations. Movement of birds from one island to another, resulting in a high rate of gene exchange, is a possible resolution of this problem, but if this is correct it raises another one: why, in the face of extensive gene flow, do the means of traits of different populations differ as much as they do?

An alternative to intraspecific gene flow is gene flow between species. Results of the long-term studies on Daphne and Genovesa showed that rare hybridization events (<1%) and ensuing gene exchange through backcrossing does increase genetic variation, thereby linking the evolutionary fate of one species to another.

The interdependence fluctuates as the direction of backcrossing changes. On Daphne it has changed from a predominant flow of genes from *G. scandens* to *G. fortis* to a predominant flow in the opposite direction. Introgression has not been balanced by loss of genetic variation through oscillating directional selection, instead in the last two decades genetic input into the *G. scandens* population has increased, and most individuals now (2005) have the genetic signature of backcrosses. Thus *G. fortis* and *G. scandens* are currently converging phenotypically and genetically, but are kept apart by song. This remarkable state of affairs has occurred through high hybrid and backcross survival rather than through an increase in hybridization.

### **Implications of Hybridization**

Exchange of genes through hybridization has interesting implications in the context of speciation. For example, it implies a dynamic tension between ecologically differentiated species that are derived from a common ancestor. This is quite different from the normal view of speciation as a steady increase in differences between populations leading eventually to the complete cessation of interbreeding.

Events on Daphne illustrate how the process of divergence can be put into reverse under certain environmental conditions. The outcome, if the process continues, is difficult to predict. We can think of four alternatives. The species could remain as they currently are, maintained as separate species by the distinctness of their songs. They could eventually fuse into a single panmictic and bilingual population as a result of an increase in frequency of hybridization each generation due to their increasing morphological similarity. Then again the environment could revert to pre-1983 conditions, in which case gene exchange could diminish, the fitness of hybrids might decline under the changed ecological conditions, the two species would diverge, returning to their respective morphological states in 1973 when we began our study.

If the environment changes, a fourth possibility is a new evolutionary trajectory guided by natural selection and facilitated by hybridization. Hybridization and

backcrossing play two facilitatory roles. As well as increasing variation, on which agents of selection can act, hybridization of species with different allometries such as *G. fortis* and *G. scandens* weakens genetic correlations between traits. This has the effect of reducing genetic constraints on novel directions of evolutionary change.

We believe these effects of hybridization could be general. Small, transitory, islands like Daphne with unique ecologies might have been arenas for introgression that facilitated novel directions of evolution and contributed to the adaptive radiation. We know that hybridization is not restricted to Daphne and Genovesa. Throughout the archipelago species are often more similar to each other genetically on the same island than on different islands, which is indicative of widespread, low-level, hybridization since species on the same island can hybridize whereas those on different islands cannot. Hybridization may have been going on episodically ever since the adaptive diversification of the ancestral finch species gave rise to two populations living in the same environment. Indeed, hybridization might have been important in the early stages of adaptive radiations in other organisms in other environments around the globe.

### **The Value of Long-term Study of a Single System**

Continuous, annually repeated, study can potentially yield more insight into the causes of change as well as more precise measures of change itself. We have gained benefits that would have eluded us if the study had been intermittent as opposed to annually continuous. Perhaps the most important finding is that long-term effects of rare but strong events can have long-lasting consequences for the environment and for the organisms that exploit it. Short-term or intermittent studies are likely to miss such events and not be able to interpret the consequences.

The best example of this phenomenon is the critical El Niño event of 1982-83 on Daphne. If we had stopped before that year we could have concluded, incorrectly, that droughts invariably select for large body and beak size, hybrids do not breed, and the island cannot support another species (e.g. *G. magnirostris*). If we had started after 1983 we would have been mystified about the origins of the current interbreeding and convergence of *G. fortis* and *G. scandens*, we would have missed the colonization by *G. magnirostris* and would have no reason to believe that it

had not always been a member of the community of breeding finches. Our appreciation of the ecological and evolutionary importance of annual environmental variation would have been much diminished.

### **Conclusions**

We conclude by emphasizing that our study, like other long-term field studies, did not progress with a steady accumulation of knowledge and understanding, on an undeviating linear trajectory. Expectations at the outset were conditioned by our understanding from reading the literature, and almost inevitably surprises were encountered on the way. El Niños and droughts were far more intense than we expected, and evolutionary change was far more rapid. We gradually became aware of the importance of song and the interaction of learned cultural and genetical evolution, a change in the fate of hybrids (and the implications for speciation), the fact that changes in vegetation as a result of changes in climate could have evolutionary consequences as well as the more obvious ecological ones, and the fact that a reversal of weather did not result in a reversal of vegetation characteristics because there is an inertia to the system. The importance of temporal scale shifted from annual to decadal. Some observations forced us to re-think theory, for example the success of inbred *G. magnirostris*. Finally, we had no basis for expecting that the populations would not be the same phenotypically and genetically at the end as they were at the beginning of the study. Ramifications of this last result are still being explored.

All of these findings have been made possible by protection and conservation of the unique biota of the Galápagos by the Galápagos National Parks Service. These efforts, occasionally opposed strenuously by commercial interests, have been aided by the Charles Darwin Foundation and the Charles Darwin Research Station on Santa Cruz Island, Galápagos, and further supported by fund-raising organizations including the Charles Darwin Foundation Inc. and Friends of Galápagos in Switzerland, Britain, and other European countries. Further understanding of evolutionary processes in the Galápagos archipelago, in marine as well as terrestrial environments, depends crucially on the continuation of such conservation efforts. By recognizing the value of research into the population biology and evolution of Darwin's finches the Balzan Prize Committee will give a boost to these efforts and, we hope, to similar efforts to conserve natural systems more broadly around the globe. For this we are deeply grateful.

## Research Project - Abstract

### 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. 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 Ramos (Ph.D. student) 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 (an island nation located in the Gulf of Guinea). 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 (Ph.D. student) tested the hypothesis that reduced genetic variation due to inbreeding 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 was 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 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.

**Statement by the Prizewinners**

With the 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, 5-6 September, 2008. 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.

**Publications:**

- Paquita E. A. Hoeck, Mark A. Beaumont, Karen E. James, Rosemary B. Grant, Peter R. Grant and Lukas F. Keller, Saving Darwin's muse: evolutionary genetics for the recovery of the Floreana mockingbird, *Biology Letters* 6: 212-215, 2010.

### **Biographical and bibliographical data**

PETER R. GRANT was born in Norwood, London, on 26 October 1936.

He is Class of 1877 Professor of Zoology Emeritus, Princeton University (since 2008).

After receiving his BA (Honors) in 1960 from Cambridge University and his Ph.D. in 1964 from the University of British Columbia, he earned a post-doctoral Fellowship at Yale University (1964-1965). At McGill University he became Assistant Professor (1965-1968), Associate Professor (1968-1973) and full Professor (1973-1977). He was Professor at the University of Michigan (1977-1985) prior to his appointment at Princeton University (1985), where he became Class of 1877 Professor of Zoology (1989). He was also Visiting Professor at the Universities of Uppsala (1981, 1985) and Lund (1981).

He is a member or a fellow of numerous US and European societies and academies, such as the Royal Society of London, the Royal Society of Canada, the American Philosophical Society, the American Academy of Arts and Sciences, the American Association for the Advancement of Science, the American Society of Naturalists (President in 1999, Honorary member since 2008), and the American Academy of Sciences. He is also a member of the Society for the Study of Evolution, the Ecological Society of America, the American Ornithologists' Union, the Linnean Society of London, the Society for Behavioural Ecology and Charles Darwin Foundation, where he is a member of the General Assembly. He received honorary degrees from the universities of San Francisco, Quito (2005), and Zurich (2008). He was and still is an associate editor of scientific journals, including *Ecology* (1968-1970), *Evolutionary Theory* (since 1973), *Biological Journal of the Linnean Society* (since 1984), and *Philosophical Transactions of the Royal Society of London* (1990-1993). He is Honorary Citizen of Puerto Bacquerizo, I. San Cristóbal, Galápagos, since 2005.

B. ROSEMARY GRANT was born in Arnside, England, on 8 October 1936.

She is Research Scholar and Professor of Zoology Emeritus, Princeton University (since 2008).

After receiving her BSc (Honors) in 1960 from Edinburgh University, Scotland, she became a Research Associate at the University of British Columbia, Canada (1960-1964), at Yale University (1964-1965), at McGill University (1973-1977) and at the University of Michigan (1977-1985). She earned her Ph.D. in 1985 from Uppsala University. At Princeton University she became Research Scholar and Lecturer (1985), and then Senior Research Scholar and Professor in the Department of Ecology and Evolutionary Biology (1997). She was Visiting Professor at the University of Zurich, Switzerland (spring-summer 2002, summer 2003).

Member of the American Academy of Arts and Sciences (1997) and of the Charles Darwin Foundation (2002), Foreign Fellow of the Royal Society of Canada (2004) and Fellow of the Royal Society of London (2007), Foreign Member of the American Academy of Sciences (2008) and honorary member of the American Society of Naturalists (2008), she received honorary degrees from McGill University (2002), Universidad San Francisco, Quito (2005), and the University of Zurich (2008). She is Honorary Citizen of Puerto Bacquerizo, I. San Cristóbal, Galápagos, since 2005.

PETER R. GRANT as well as B. ROSEMARY GRANT were awarded on 12 February 2009, the Darwin-Wallace Medal of 2009 of the Linnean Society of London on the occasion of Charles Darwin's 200th birthday, 12 February, 2009.

They have received several joint honours, including the 2009 Kyoto Prize for the category of Basic Sciences, the Municipality of Puerto Ayora Science Award, I. Santa Cruz, Galápagos (2006), the American Institute of Biological Sciences Outstanding Scientist Award for 2005, the Distinguished Scientists Award for 2005 from the American Institute of Biological Sciences, the Grinnell Award from the University of California at Berkeley (2003), the Loye and Alden Miller Award from the Cooper Ornithological Society (2003), the Darwin Medal from the Royal Society of London (2002), the E.O. Wilson Prize from the American Society of Naturalists (1998) and the Leidy Medal from the Academy of Natural Sciences of Philadelphia (1994).

For their book *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos* (Chicago, University of Chicago Press, 1989) they received the Wildlife Society's 1991 Wildlife Publication Award. The book by Jonathan Weiner, *The Beak of the Finch: A Story of Evolution in Our Time* (New York, Al-

fred Knopf, 1994), in which Rosemary and Peter Grant discuss their 20 years of fascinating research, was awarded in 1995 the Pulitzer Non-Fiction Prize. Their most recent book *How and Why Species Multiply. The radiation of Darwin's Finches* (Princeton University Press, Princeton, New Jersey) was published in 2008. Their new book *In Search of the Causes of Evolution. From Field Observations to Mechanisms* (Princeton University Press, Princeton, NJ), is in press.

They advised the California Science Center in constructing an Evolution Exhibit featuring Darwin's Finches and their research on them, as well as the exhibit entitled "Explore Evolution" sponsored by the National Science Foundation, and the American Museum of Natural History "Darwin" exhibit.

Peter and Rosemary Grant have jointly published numerous journal papers. Among the most recent we mention:

- Saving Darwin's muse: evolutionary genetics for the recovery of the Floreana mockingbird, *Biology Letters* 6: 212-215, 2010 (with others)
- Conspecific versus heterospecific gene exchange between populations of Darwin's finches. *Philosophical Transactions of the Royal Society B* 365: 1065-1076, 2010
- Multilocus genotypes from Charles Darwin's finches: biodiversity lost since the voyage of the Beagle. *Philosophical Transactions of the Royal Society B* 365: 1009-1018, 2010 (with others)
- Ecoimmunity in Darwin's finches: invasive parasites trigger acquired immunity in the medium ground finch (*Geospiza fortis*). *PLoS one* 5(1): e8605, 2010 (with others)
- Darwin's finches: studying evolution in action. Pp. 122-129 in T. de Roy (ed.), *Galápagos. Preserving Darwin's Legacy*. David Bateman Ltd., Auckland, 2009
- The secondary contact phase of allopatric speciation in Darwin's finches. *Proceedings of the National Academy of Sciences USA* 106: 20141-20148, 2009
- Sympatric speciation, immigration and hybridization in island birds. Pp. 326-357 in *The theory of island biogeography revisited*, J. Losos and R. E. Ricklefs (eds.). Princeton University Press, Princeton, 2009
- Fission and fusion of Darwin's finch populations. *Philosophical Transactions of the Royal Society B* 363: 2821-2829, 2008
- Pedigrees, assortative mating and speciation in Darwin's finches. *Proceedings of the Royal Society B* 275: 661-668, 2008

## International Balzan Foundation

The International Balzan Foundation was established in Lugano in 1956 thanks to the generosity of Lina Balzan who had come into a considerable inheritance on the death of her father, Eugenio. She destined this wealth to honour her father's memory.

Eugenio Francesco Balzan was born in Badia Polesine, near Rovigo (Northern Italy), on 20 April 1874 to a family of landowners. He spent almost his entire working life at Milan's leading daily paper *Corriere della Sera*. After joining the paper in 1897, he worked his way up, from editorial assistant, to editor-in-chief and then special correspondent\*. In 1903 editor Luigi Albertini made him managing director of the paper's publishing company; he then became a partner and shareholder in the company. He was not only a clever and skilful manager but also a leading personality in Milan. In 1933 he left Italy due to opposition from certain milieus hostile to an independent *Corriere*. He then moved to Switzerland, living in Zurich or Lugano, where for years he had invested his fortune with success. He also continued his charitable activities in favour of institutions and individuals.

After returning to Italy in 1950, Eugenio Balzan died in Lugano, Switzerland, on 15 July 1953.\*\*

Today, the Balzan Foundation, international in character and scope, acts jointly through two Foundations: one under Italian law and the other under Swiss law.

In Milan, the *International E. Balzan Prize Foundation* – “Prize” has the aim to promote, throughout the world, culture, science, and the most meritorious initiatives in the cause of humanity, peace and brotherhood among peoples, regardless of nationality, race or creed. This aim is attained through the annual award of prizes in two general fields: literature, the moral sciences and the arts; medicine and the physical, mathematical and natural sciences.

Nominations for the prizes in the scientific and humanistic fields are received at the Foundation's request from the world's leading learned societies. Candidates are selected by the *General Prize Committee*, composed of eminent European scholars and scientists. Since 2001, each prize is worth one million Swiss francs, half of which the prizewinner must destine for research work, preferably involving young researchers.

At intervals of not less than three years, the Balzan Foundation also awards a “Prize for Humanity, Peace and Brotherhood among Peoples”, of varying amounts.

In Zurich, the *International E. Balzan Prize Foundation* – “Fund” collects, protects and administers Eugenio Balzan's estate so as to place at the disposal of the International E. Balzan Prize Foundation – “Prize” the necessary financial means to realize its objective.

\* Renata Brogginì (a cura di), *Eugenio Balzan. L'emigrazione in Canada nell'inchiesta del “Corriere”*. 1901, Fondazione Corriere della Sera, Milano, 2009.

\*\* Renata Brogginì, *Eugenio Balzan 1874-1953. Una vita per il “Corriere”, un progetto per l'umanità*, RCS Libri, Milano, 2001.

Renata Brogginì, *Eugenio Balzan 1874-1953. A Biography*, Hoepli, Milano, 2007.

**Members of the International Balzan Foundation**  
(March, 2010)

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Erwin Neher (Germany)  
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Dmitry O. Shvidkovsky (Russia)  
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Arina Kowner (Switzerland)



**Balzan Prizewinners  
for literature, moral sciences, and the arts,  
for physical, mathematical and natural sciences, and medicine**

2009	<b>TERENCE CAVE</b> (UK) <b>MICHAEL GRÄTZEL</b> (Switzerland/Germany) <b>BRENDA MILNER</b> (Canada/UK) <b>PAOLO ROSSI MONTI</b> (Italy)	Literature since 1500 The Science of New Materials Cognitive Neurosciences History of Science
2008	<b>WALLACE S. BROECKER</b> (USA) <b>MAURIZIO CALVESI</b> (Italy) <b>IAN H. FRAZER</b> (Australia/UK)  <b>THOMAS NAGEL</b> (USA/Serbia)	Science of Climate Change The Visual Arts since 1700 Preventive Medicine, including Vaccination Moral Philosophy
2007	<b>ROSALYN HIGGINS</b> (UK) <b>SUMIO IJIMA</b> (Japan) <b>MICHEL ZINK</b> (France) <b>JULES HOFFMANN</b> (France) and <b>BRUCE BEUTLER</b> (USA)	International Law since 1945 Nanoscience European Literature, 1000-1500 Innate Immunity
2006	<b>LUDWIG FINSCHER</b> (Germany) <b>QUENTIN SKINNER</b> (UK) <b>PAOLO DE BERNARDIS</b> (Italy) and <b>ANDREW LANGE</b> (USA) <b>ELLIOT MEYEROWITZ</b> (USA) and <b>CHRISTOPHER SOMERVILLE</b> (USA/Canada)	History of Western Music since 1600 Political Thought; History and Theory Observational Astronomy and Astrophysics Plant Molecular Genetics

2005	<b>PETER HALL</b> (UK)	The Social and Cultural History of Cities since the Beginning of the 16 <sup>th</sup> Century
	<b>LOTHAR LEDDEROSE</b> (Germany)	The History of the Art of Asia
	<b>PETER and ROSEMARY GRANT</b> (USA/UK)	Population Biology
	<b>RUSSELL HEMLEY</b> (USA) and <b>HO-KWANG MAO</b> (USA/China)	Mineral Physics
2004	<b>PIERRE DELIGNE</b> (USA/Belgium)	Mathematics
	<b>NIKKI RAGOZIN KEDDIE</b> (USA)	The Islamic world from the end of the 19 <sup>th</sup> to the end of the 20 <sup>th</sup> century
	<b>MICHAEL MARMOT</b> (UK)	Epidemiology
	<b>COLIN RENFREW</b> (UK)	Prehistoric Archaeology
2003	<b>REINHARD GENZEL</b> (Germany)	Infrared Astronomy
	<b>ERIC HOBBSAWM</b> (UK/Egypt)	European History since 1900
	<b>WEN-HSIUNG LI</b> (USA/Taiwan)	Genetics and Evolution
	<b>SERGE MOSCOVICI</b> (France/Romania)	Social Psychology
2002	<b>WALTER JAKOB GEHRING</b> (Switzerland)	Developmental Biology
	<b>ANTHONY THOMAS GRAFTON</b> (USA)	History of the Humanities
	<b>XAVIER LE PICHON</b> (France/Vietnam)	Geology
	<b>DOMINIQUE SCHNAPPER</b> (France)	Sociology
2001	<b>JAMES SLOSS ACKERMAN</b> (USA)	History of Architecture (including town planning and landscape design)
	<b>JEAN-PIERRE CHANGEUX</b> (France)	Cognitive Neurosciences
	<b>MARC FUMAROLI</b> (France)	Literary History and Criticism (post 1500)
	<b>CLAUDE LORIUS</b> (France)	Climatology

- 2000 **ILKKA HANSKI** (Finland) Ecological Sciences  
**MICHEL MAYOR** (Switzerland) Instrumentation and Techniques  
in Astronomy and Astrophysics  
**MICHAEL STOLLEIS** (Germany) Legal History since 1500  
**MARTIN LITCHFIELD WEST** (UK) Classical Antiquity
- 1999 **LUIGI LUCA CAVALLI-SFORZA** Science of Human Origins  
(USA/Italy)  
**JOHN ELLIOTT** (UK) History, 1500-1800  
**MIKHAEL GROMOV** Mathematics  
(France/Russia)  
**PAUL RICŒUR** (France) Philosophy
- 1998 **HARMON CRAIG** (USA) Geochemistry  
**ROBERT MCCREDIE MAY** Biodiversity  
(UK/Australia)  
**ANDRZEJ WALICKI** (USA/Poland) History: The cultural and social history  
of the Slavonic world from the reign  
of Catherine the Great to the Russian  
revolutions of 1917
- 1997 **CHARLES COULSTON GILLISPIE** (USA) History and Philosophy of Science  
**THOMAS WILSON MEADE** (UK) Epidemiology  
**STANLEY JEYARAJA TAMBIAH** Social Sciences: Social Anthropology  
(USA/Sri Lanka)
- 1996 **ARNO BORST** (Germany) History: Medieval Cultures  
**ARNT ELIASSEN** (Norway) Meteorology  
**STANLEY HOFFMANN** Political Sciences:  
(France/USA/Austria) Contemporary International Relations

- 1995 **YVES BONNEFOY** (France) Art History and Art Criticism  
(as applied to European Art from  
the Middle Ages to our times)
- CARLO M. CIPOLLA** (Italy) Economic History
- ALAN J. HEEGER** (USA) Science of New Non-Biological  
Materials
- 1994 **FRED HOYLE** (UK) and Astrophysics (evolution of stars)  
**MARTIN SCHWARZSCHILD**  
(USA/Germany)
- RENÉ COUTEAUX** (France) Biology (cell-structure with special  
reference to the nervous system)
- NORBERTO BOBBIO** (Italy) Law and Political Science  
(governments and democracy)
- 1993 **WOLFGANG H. BERGER** Paleontology with special reference  
(USA/Germany) to Oceanography
- LOTHAR GALL** (Germany) History: Societies of the 19<sup>th</sup> and  
20<sup>th</sup> centuries
- JEAN LECLANT** (France) Art and Archaeology of the  
Ancient World
- 1992 **ARMAND BOREL** (USA/Switzerland) Mathematics
- GIOVANNI MACCHIA** (Italy) History and Criticism of Literatures
- EBRAHIM M. SAMBA** (Gambia) Preventive Medicine
- 1991 **JOHN MAYNARD SMITH** (UK) Genetics and Evolution
- GYÖRGY LIGETI** Music  
(Austria/Hungary/Romania)
- VITORINO MAGALHÃES GODINHO** History: The emergence of Europe  
(Portugal) in the 15<sup>th</sup> and 16<sup>th</sup> centuries

- 1990 **PIERRE LALIVE D'EPINAY** (Switzerland) Private International Law  
**JAMES FREEMAN GILBERT** (USA) Geophysics (solid earth)  
**WALTER BURKERT** (Germany) Study of the Ancient World  
(Mediterranean area)
- 1989 **MARTIN JOHN REES** (UK) High Energy Astrophysics  
**LEO PARDI** (Italy) Ethology  
**EMMANUEL LÉVINAS** (France/Lithuania) Philosophy
- 1988 **MICHAEL EVENARI** (Israel/France) and Applied Botany  
**OTTO LUDWIG LANGE** (Germany) (including ecological aspects)  
**RENÉ ETIEMBLE** (France) Comparative Literature  
**SHMUEL NOAH EISENSTADT** Sociology  
(Israel/Poland)
- 1987 **PHILLIP V. TOBIAS** (South Africa) Physical Anthropology  
**JEROME SEYMOUR BRUNER** (USA) Human Psychology  
**RICHARD W. SOUTHERN** (UK) Medieval History
- 1986 **JEAN RIVERO** (France) Basic Human Rights  
**OTTO NEUGEBAUER** (USA/Austria) History of Science  
**ROGER REVELLE** (USA) Oceanography/Climatology
- 1985 **ERNST H.J. GOMBRICH** History of Western Art  
(UK/Austria)  
**JEAN-PIERRE SERRE** (France) Mathematics
- 1984 **JAN HENDRIK OORT** (Netherlands) Astrophysics  
**SEWALL WRIGHT** (USA) Genetics  
**JEAN STAROBINSKI** (Switzerland) History and Criticism of Literatures

1983	<b>FRANCESCO GABRIELI</b> (Italy)	Oriental Studies
	<b>ERNST MAYR</b> (USA/Germany)	Zoology
	<b>EDWARD SHILS</b> (USA/UK)	Sociology
1982	<b>JEAN-BAPTISTE DUROSELE</b> (France)	Social Sciences
	<b>MASSIMO PALLOTTINO</b> (Italy)	Sciences of Antiquity
	<b>KENNETH VIVIAN THIMANN</b> (USA/UK)	Pure and Applied Botany
1981	<b>JOSEF PIEPER</b> (Germany)	Philosophy
	<b>PAUL REUTER</b> (France)	International Public Law
	<b>DAN PETER MCKENZIE,</b> <b>DRUMMOND HOYLE MATTHEWS</b> and <b>FREDERICK JOHN VINE</b> (UK)	Geology and Geophysics
1980	<b>ENRICO BOMBIERI</b> (USA/Italy)	Mathematics
	<b>JORGE LUIS BORGES</b> (Argentina)	Philology, Linguistics and Literary Criticism
	<b>HASSAN FATHY</b> (Egypt)	Architecture and Urban Planning
1979	<b>JEAN PIAGET</b> (Switzerland)	Social and Political Sciences
	<b>ERNEST LABROUSSE</b> (France) and <b>GIUSEPPE TUCCI</b> (Italy), <i>ex aequo</i>	History
	<b>TORBJÖRN CASPERSSON</b> (Sweden)	Biology
1962	<b>KARL VON FRISCH</b> (Austria)	Biology
	<b>ANDREJ KOLMOGOROV</b> (Russia)	Mathematics
	<b>PAUL HINDEMITH</b> (Germany)	Music
	<b>SAMUEL ELIOT MORISON</b> (USA)	History

**Balzan Prizewinners  
for Humanity, Peace and Brotherhood among Peoples**

- 2007 **KARLHEINZ BÖHM** (Austria/Germany)
- 2004 **COMMUNITY OF SANT'EGIDIO**
- 2000 **ABDUL SATTAR EDHI** (Pakistan/India)
- 1996 **INTERNATIONAL COMMITTEE OF THE RED CROSS**
- 1991 **ABBÉ PIERRE** (France)
- 1986 **UNITED NATIONS REFUGEE AGENCY (UNHCR)**
- 1978 **MOTHER TERESA OF CALCUTTA** (India/Macedonia)
- 1962 **POPE JOHN XXIII** (Vatican City/Italy)
- 1961 **NOBEL FOUNDATION**

