# Frontiers in Population Biology

REPORT OF A POPULATION BIOLOGY TASK FORCE

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# **INTRODUCTION**

Support for environmental research will be a priority for NSF for the immediate future. Practically, this means new funds will be available and new programs will be developed. Some areas likely to receive funding are becoming clearer under the umbrella of biocomplexity (e.g. Mervis 1998. Science 281:1944-1945, 1947), but specific foci for new investments are still being defined. In October 1998 a panel of experts met at NSF to identify leading research areas in population biology that merited special investment.

Ultimately, the responsibility for converting the recommendations of the research community into programmatic initiatives and budgetary allocations falls to NSF's program officers. Indeed, the funding profile of different areas can and does evolve in response to dynamics of proposal submissions and Panel recommendations, with current topical areas receiving special emphasis (see Appendix 1). However, this process, while responsive to the scientific community, does not reflect directed awareness of targeted research areas that may be particularly timely in terms of potential for scientific advance.

The convening of this task force is a mark of the interest of the officers in Population Biology in having more focused advice from the research community to shape their program. This level of strategic thinking was encouraged by Division Director Bruce Hayden in order to align program elements within the Division of Environmental Biology with major cross-directorate initiatives, like biocomplexity, which will be major sources of future funding. It is a timely strategy that reflects the increasing importance of environmental research and the increasing degree to which research in this area is multidisciplinary, interdisciplinary, and integrative.

This task force is related to the ongoing initiative on "Evolution, science, and society." The ESS project has generated a pair of documents (an Executive Summary & a more detailed Executive Document) intended to promote awareness of the scientific potential for the field of evolutionary biology in the science policy community. These documents have been posted on the web (via www.amnat.org), where information for obtaining hard copies is available. The Executive Summary was reproduced in the November 1999 issue of BioScience, and the longer Executive Document will be reproduced in a forthcoming issue of The American Naturalist. In addition to providing input to the science policy community, an additional goal of the ESS project is to generate broader interest and awareness of the potential of various aspects of evolutionary biology to the scientific community itself. Thus, it is our intention that efforts such as the present task force report can be viewed as a potential research agenda for the field of population biology. It is also the intention of

the ESS project, and in particular this task force report, to stimulate ongoing review, reassessment, and reevaluation of the scientific goals of population biology.

The task force had three specific goals:

- To identify research areas deserving investment as special areas of focused research;
- To suggest mechanisms for incorporating these initiatives into NSF's research priorities;
- To summarize the task force's recommendations for NSF and the research community.

# RESEARCH THEMES

The task force meeting consisted of a series of group sessions to identify overall research themes, with sub-groups charged with responsibility for providing more definition to each research theme identified. A final group session was directed towards achieving balance and concensus. The following research themes came out of these deliberations.

# Divergence of genetic architectures

# Definition:

Genetic architecture refers to the number, arrangement, and pattern of interaction among genes that influence expression of a trait

### Rationale:

Populations evolving independently of one another are expected to diverge, and changes in allele frequencies are only part of the way in which they may diverge. The effect of allelic variation at any single locus commonly depends on both the environment in which that variation is expressed and on allelic variation at other loci. Much of our current ability to link micro-evolution to macro-evolution is, however, based on the assumption that genetic architecture is relatively stable, i.e., that evolutionary changes are largely accounted for by changes in the frequency of alleles rather than by changes in the pattern of allelic interaction among loci. Theoretical work has shown that traditional approaches are adequate for quantitative predictions only within the environment in which measurements are made and only for a small number of generations. Recent technical advances have made it possible to investigate changes in genetic architecture at a variety of scales. Thus, we can determine the scale at which it is reasonable to presume that genetic architecture is relatively stable and subsequently investigate the extent to which the evolution of genetic architecture constrains population divergence and speciation or, conversely, is itself constrained by natural selection or other evolutionary forces.

# Examples:

- To what extent does the genetic architecture change when traits are subject to selection? Is there a predictable relationship between the strength of selection and the rate at which the architecture changes over time? Does the genetic architecture change in similar ways for different sets of traits, or is the pattern of change specific to the particular set of traits being investigated? To what extent do closely related species exhibit similar changes in the genetic architecture in response to similar selection pressures?
- To what extent is the genetic architecture of traits similar among populations and closely related species? To what extent do QTL maps or genetic variance-covariance matrices of traits depend on the population or environment in which they are measured? To what extent do dominance and epistatic interactions among QTLs depend on the population or environment in which they are measured? What is the relationship between genetic architecture, as revealed by analysis of QTLs, the genetic variance-covariance matrix, and short- and long-term evolutionary responses to selection?
- To what extent does the genetic architecture constrain evolutionary divergence among populations? Do some patterns of intra- and inter-locus allelic interactions allow more rapid divergence of populations subject to divergent selection pressures than do others? Can the potential for differential response be predicted from knowledge of the genetic variance-covariance matrix, from QTL maps, or from other measures of genetic architecture?
- What are the processes by which genetic architectures of populations and species diverge from one another and to what extent are they unable to diverge? Are differences primarily quantitative at low levels of the evolutionary hierarchy (e.g., differences among populations or within metapopulations) becoming progressively more qualitative at higher levels (e.g., hybridizing populations or species)? How is the extent of introgressive gene flow between divergent populations influenced by differences in genetic architecture? Are populations differing substantially in genetic variance-covariance matrices or in QTL patterns less likely to be influenced by introgressive gene flow than those that are similar? To what extent does gene flow among populations prevent divergence in genetic architectures?

# Genetic architecture and evolutionary trajectories

### Definition:

Genetic architecture refers broadly to the set of the properties of genes and their interactions (including epigenetic effects) that determine the phenotype of an organism.

### Rationale:

One of the primary tenets of evolutionary biology is that the genetic architecture often directs and constrains evolutionary change. Quantitative genetics has provided one level of description of this principle by equating constraint with genetic correlations among traits. This approach has been successful at predicting short-term evolutionary change. However, it does not provide a prediction of what correlations any individual species will exhibit.

Despite the fact that it is well established that rates of evolution vary substantially among genes, very little is understood about what aspects of the genetic architecture (e.g., variation among genes in degree of pleiotropy) are responsible for the selective constraints that doubtless explain much of this variation. At the same time, through decades of work on a variety of model genetic systems, we have learned a tremendous amount about the functions of individual genetic products and their integration into biochemical pathways. More recently, this work has been extended to sequencing entire genomes. This wealth of descriptive information requires an organizing principle that can be provided by an evolutionary perspective. Furthermore, such a perspective allows a synthesis of all this information to assist in explaining and predicting the kinds of constraints on complex phenotypes (e.g., development, physiology, and behavior) that will be imposed by the genetic architecture.

- How does genetic architecture influence the rate and direction of evolutionary change?
- What are the relative roles of regulatory versus structural genes in evolution? Can these relative roles be explained by differences in the degree to which regulatory and structural genes are constrained?
- How pervasive are pleiotropy and epistasis? What are the influences of these complexities on the evolution of quantitative traits? What are the underlying molecular, biochemical, and physiological bases of these complexities?
- Is evolution predisposed to certain trajectories based on the underlying genetic architecture?
- To what extent do the answers to the above questions depend on the stability of the genetic architecture over time? By stability we mean that changes occur in the array of alleles at a locus, the arrays of alleles among loci, the physical arrangement of those loci, and the numbers of copies of those alleles and loci. A fruitful approach to answer this question is to contrast systems that differ in these properties or how fluid they are, such as: sexual versus asexual reproduction, haploid versus diploid versus polyploid, inbred versus outbred, high versus low mutation rates, population structure.

- To what extent do the answers depend on the organism's environment, both internal and external?
- To what extent does the position or relative rate coefficient of an enzyme in a biochemical pathway influence selective constraint, and hence rate of sequence evolution?

# The evolution of complex phenotypes

### Definition:

Complex phenotypic characters are determined by interaction of multiple causes. Such characters represent a challenge to developmental evolutionary biologists because there are typically no readily apparent intermediate phenotypes that would be likely to be maintained by selection. The classic example is the vertebrate eye.

### Rationale:

One of the principal problems facing evolutionary biology is explaining the evolution of novel, complex phenotypes. Our current molecular and genetic understanding of both the process of development and the organization of biochemical pathways suggests that the time is ripe for an attempt to document and explain the evolutionary processes that give rise to complex phenotypes. Knowledge of those processes should also yield insight into how the genetic architecture directs and constrains evolutionary change.

# Examples:

- To what extent can microevolutionary processes explain the evolution of complex phenotypes?
- What principles govern the evolutionary dynamics of changes in gene regulation?
- What is the role of gene duplication, genome rearrangement, genome duplication, and hybridization in generating phenotypic novelty?
- Are there new evolutionary principles to be revealed by the comparative study of development?
- Can our understanding of the dynamics of the genotypephenotype mapping inform us about macroevolutionary trends?
- Is the evolution of novel, complex traits likely to involve allelic substitutions or novel genetic effects?

# **Evolving symbioses**

# Definition:

Symbioses are pairs (and larger sets) of organisms living in extremely close and often obligate association. Such associations include a wide-range of hosts and parasites, from the transposons and viruses that reside in all chromosomes to plants and herbivores. In some cases, vector organisms are

necessary to shuttle parasites among multiple host species. Symbioses also include myriad mutualistic interactions, from intracellular organelles derived from once free-living microorganisms all the way to plants and pollinators. Understanding the evolutionary origins and mechanisms of change in symbiotic associations requires integration of new genetic information and ecological expertise.

### Rationale:

To date, the best-studied interactions have been infectious diseases, which have traditionally been studied from biomedical and agricultural perspectives. Most of this work has focused on elucidating the molecular bases of pathogenicity and susceptibility. But the evolution of pathogenicity and susceptibility are not well understood, and such a perspective will provide important new insights for understanding and managing host-pathogen interactions. Moreover, pathogenic interactions are only one class among many symbioses, which take a variety of forms and are involved in such important yet poorly understood evolutionary phenomena as the generation of biodiversity and the emergence of biocomplexity. New discoveries have shown, for example, that both inter and intra genomic interactions can promote population divergence and speciation.

- Why are some parasites (very broadly interpreted, from viruses to herbivores) so highly virulent to their hosts whereas close relatives are more benign? Molecular biologists have had great success in identifying the genetic bases of virulence, but the evolutionary forces that have led to such diversity in levels of virulence are poorly understood.
- How does the genetic architecture (number of genes, patterns of dominance, pleiotropy) of parasite virulence and host resistance influence ecological and evolutionary dynamics of the interaction?
- How do changes in host population density and spatial pattern influence the evolution of parasites?
- What is the relationship between genetic and phenotypic diversity in a host population and its susceptibility to invasion and epidemics of parasites? How does host diversity in turn influence parasite evolution (broad or narrow host range, high or low mutation rate, etc.)?
- What ecological conditions and genetic processes permit the origin of new symbioses? What conditions and processes promu(e major changes in symbioses, for example, the evolution of mutualistic associations from formerly exploitative interactions?

- What are the various forms of conflict among different genomic elements (e.g. transposons and chromosomes, genes mediating conflict between male and female reproductive success, meiotic drivers, role of endosymbiotic microbes in determining sex-ratio, mating compatibility, etc)? How have these conflicts arisen, and how have they been ameliorated or otherwise modified by subsequent evolution?
- Can symbiotic associations be engineered for new applications in managed ecosystems (e.g., meiotic drivers for biocontrol, novel symbioses for bioremediation)?

# **Biology of invasive species**

# Definition:

Invasive species are those that are undergoing dramatic ecological and/or geographic range expansions, often as a result of human influence.

### Rationale:

Change is a fundamental characteristic of all species and communities, but there are many features of how change affects species and communities that are not understood at a basic level. Despite this lack of understanding, as a result of human actions, an increasing number of species are being introduced in new areas at an unprecedented scale. Global warming, habitat fragmentation, and urbanization promote the dispersal of species. There have already been major impacts on species and communities, and this impact will undoubtedly increase. These introductions provide an opportunity to investigate traditional forces such as migration, genetic diversity, and adaptation to predict the outcome of future introductions.

# Examples:

- Are species invasions primarily a consequence of simply increased dispersal, genetic change in the invading species, phenotypic flexibility of the invading species, change in the species or structure of the community invaded, or environmental change that alters the community's susceptibility to invasion?
- Are there qualitative differences in "natural" versus humanmediated invasions?
- What are the characteristics of species that make them vulnerable to extinction as a result of species introductions?
- How does the invasiveness of species depend on the biocomplexity of the invaded community?
- Will the study of range expansion lead to a better understanding of mechanisms of invasion?

# **Community genetics**

Understanding the causes and consequences of biodiversity and biocomplexity requires integrating information about processes occurring at different organizational levels, from the gene to populations, species, communities, and ecosystems. In a practical sense, this integration will be increasingly important for understanding biotic responses to environmental perturbations at all levels, from the invasion of single species to global change. From a basic perspective, an initiative in the general area of community genetics would be valuable. It would bring together ecologists who work on multi-species systems with an emphasis on phenotypes, and evolutionary biologists with a tradition of working on the genetics of single species. These complementary approaches forge a common conceptual framework for understanding the generation and maintenance of biodiversity.

### Definition:

Community composition and dynamics, and associated functional 'roles' of species within an ecosystem, are the result of evolutionary and coevolutionary changes within and among individual species.

### Rationale:

Global change is placing unprecedented stresses on organisms and it is almost certain that one response to this stress will be evolutionary changes in many species. Currently we have little understanding of how these evolutionary changes feed back to alter community composition and ecosystem function. Understanding this feedback should (1) provide possible methods for managing the relative abundance of desirable *versus* undesirable species in communities and (2) provide greater understanding of the processes determining biodiversity, biocomplexity, and ecosystem function.

- Under what circumstances does invasion by or extinction of a particular species cause evolutionary change in associated species that leads to alteration of community and ecosystem dynamics?
- Are emergent diseases (*e.g.* those associated with amphibian decline) primarily a consequence of evolutionary change in the pathogen, evolutionary change in the host, or environmental change that alters host susceptibility?
- Do evolutionary responses of plants to elevated levels of CO<sub>2</sub> affect the performance of associated pathogens and herbivores and, if so, how do these changes in turn affect community composition?

# **Evolution in human-dominated systems**

Throughout history, humans have had an impact on their surroundings, either through intended changes, such as urban development, or inadvertent consequences of human activity, such as pollution. With population growth, the scale and pace of human impacts has increased to such a degree that it is no longer practical, and might indeed be detrimental, to make a distinction between "natural" and human perturbed systems. People do not exist separately from their environment. Indeed, the future of our biotic environment depends on how organisms respond to current and anticipated anthropogenic impacts. Thus, it is critical that we understand how organisms respond to and evolve within human dominated systems.

Human-dominated systems also offer unique opportunities for evolutionary biologists. Such systems are unlikely to be in evolutionary equilibrium, yet at the same time they are potentially simpler and tractable. Human-dominated systems thus may offer evolutionary biologists opportunities to examine how evolution is currently occurring in a system that can be manipulated.

# **Evolutionary consequences of urbanization**

### Definition:

Urbanization refers to landscape transformation associated with development for human use and habitation, including cities and adjacent suburban areas.

# Rationale:

There is a growing awareness that urban and suburban settings represent a habitat type in which biological principles operate just as they do in any other habitat. For example, organisms undergo genetic changes and evolutionary response to strong selection pressures and specific circumstances that occur in urban settings. Unique features of urban sites are that the scale and ongoing pace of disturbance is extremely high, and that the environment itself is novel to most organisms that occur there. Furthermore, urban settings are not fixed, and even the basic features of urban environments continue to change. Urban settings are non-equilibrium settings; species and patches are chasing a moving target. Finally, there is an increasing percentage of the US population living in urban environments. Well-articulated examples of the fact that evolution is taking place in the immediate midst of these populations would lend immediacy to education and public understanding of science and would serve as a reminder that we are still part of a larger biological world.

# Examples:

■ Are there "urban ecotypes" of widespread species? Urban settings present very specific challenges, even to familiar and widespread organisms. A few examples of such challenges include habitat restriction and fragmentation, rapid rates of disturbance, localized pollution, a "heat island" effect, shifts in hydrology, etc. It seems likely that these challenges

- would result in specific adaptations, leading to the formation of specialized ecotypes.
- Are species that have successfully invaded urban settings preadapted in some way; i.e., are there traits that are exhibited in surrounding environments that enable some species to successfully invade urban environments? Understanding the nature of such preadaptive traits may allow us to manipulate the populations toward specific goals.
- What are the dynamics of biodiversity in urban settings over time? We tend to think of a loss of biodiversity in such settings, but as more organisms adapt to urban circumstances, there may be a gradual rise in species composition. Also, with cycles of development, there are shifts in species distributions within urban environments that accelerate rates of colonization and local extinction in an urban metapopulation system. This line of thinking leads to a series of additional questions relating to changes in biodiversity over time:
- What regulates biotic diversity in urban settings?
- How many species are there?
- What makes species urban?
- Are species in an urban setting genetically depauperate?
- Do species compositions change over time?

# **Evolution in agricultural landscapes**

### Definition:

Agricultural landscapes include areas under cultivation, associated human habitation, and adjacent uncultivated (feral) habitats.

# Rationale:

Evolutionary biologists are now in the position to help in design of more sustainable agricultural systems. At the same time evolutionary biologists can profit from the opportunity to work in systems that can be more precisely manipulated than unmanaged systems, and are more complex than laboratory systems.

Since the publication of Rachel Carson's "Silent Spring" there have been renewed and increased efforts to understand the ecology of agricultural systems and their impact on surrounding habitats. Efforts to decrease reliance on pesticides and move toward ecologically based pest management (NAS1996) have required agricultural scientists to develop a quantitative understanding of how organisms associated with crop production interact with each other and crop yield. There is now a substantial set of data demonstrating how factors such as shifts in crop species, landscape patterns of crop fields, cultivation practices, and introductions of biological control agents, can impact population dynamics of pest species and the

more general structure of organismic communities within the agricultural system. There has also been increasing interest in how species associated with agricultural landscapes adapt to rapid changes in these landscapes. Beyond the plethora of examples of pests becoming resistant to pesticides, there are an increasing number of cases where pest species have adapted to changes in crop rotation patterns, crop plant defense mechanisms, and biological control organisms.

Until recently, most of the research on evolutionary change in crop –associated organisms has been of a descriptive nature. There is growing recognition of the need to increase our ability to predict how organisms will respond to innovations in agriculture. Further, there is a desire to develop agricultural systems that inhibit pest adaptation or even cause self-destruction of pest species.

# Examples:

- How do weeds adapt to crop rotation?
- How can insects adapt to artificial pheromones?
- Are resistant species genetically isolated and hence inbred?
- How have organisms evolved to precipitous changes on a landscape scale (e.g. no-till and genetically engineered crops; introduction of new crops; new pollinators; soybean, sunflower, canola—herbivores/pollinator community)?
- How have organisms that rely on crop systems adapted to agricultural landscapes (e.g., quail in crops that have been engineered to resist pests that normally provide food)?
- What is the genetic architecture of changes introduced in agricultural species (e.g., pesticide resistance carries with it changes in other parts of the genome that may modify fitness effects.)?

# **Applied evolution**

# Definition:

As human-dominated systems have developed, there are increasing opportunities to make use of evolutionary principles either to achieve desired management goals or to apply evolution in the development of novel products or processes.

### Rationale:

With the rapidly expanding scale of human impacts on the biosphere, an increasing range of habitats and ecosystems are either designed and constructed for human use or have come under management as part of a broader landscape. The world is changing, and will continue to change, but to an increasing degree, human impacts are the basis for that change, and human endeavor will be impacted by those changes. Evolutionary biology directly addresses change and adaptation. It is becoming increasingly important that we apply evolutionary principles to come to grips with both intended and unintended consequences of human activities.

- Can we make economically useful predictions by applying evolutionary principles? There is a well-developed body of evolutionary theory that could be applied to managed systems to make predictions. However, guidelines and criteria for appropriate metrics and scales of measurement need to be developed.
- What are the short and long-term population and evolutionary dynamics of introduced species and varieties? Evolutionary biology has become a growing component of risk assessment in the introduction of genetically engineered organisms and other novel varieties introduced into the environment. Thus far, the focus has been on risk assessment of new invasive species that might emerge either from introgressive hybridization of transgenes into surrounding populations or escape from cultivation of transgenic organisms themselves. Such information has been gathered for specific applications, but we need a better understanding of the evolutionary dynamics of invasiveness in order to make more effective use of that information in specific applications.
- Evolutionary principles can be used to identify potentially useful adaptations for amelioration of environmental contamination or damage. For example, metal tolerant plants, initially studied as a model of an emergent novel character in natural populations, play an important role in restoration efforts in areas contaminated with heavy metals. Such plants may play an important future role in environmental cleanup. Similarly, the evolutionary relationships among different biochemical processes in microorganisms can facilitate the development of strains of bacteria to facilitate breakdown of toxic organic compounds or other environmental pollutants through bioremediation.
- We need to understand the evolution of antibiotic resistance and the emergence of novel diseases. As a result of selection pressures imposed by the widespread use of antibiotics in recent decades, evolution of antibiotic resistance has become widespread. As a result, disease that had been all but eliminated, such as tuberculosis, are reemerging as a serious medical threat. We need to understand how selection acts on microorganisms in a broad sense as well as how they are compartmentalized in our environment and within our bodies. The objective is nothing less than trying to recapture and sustain one of the most effective tools of modern medicine. At the same time, evolutionary methods can increase our understanding of the origination and early spread of new diseases, both in terms of applying phylogenetic methodology to epidemiological studies, as has been done for HIV, but also in terms of identifying organisms that may be predisposed towards evolving into pathogens.

# **CONCLUSION**

The research themes identified by the task force fell into two broad categories, with linkages to genomics & molecular genetics on the one hand and environmental issues on the other (see table below). Throughout the discussion, there were several criteria that were addressed, including: potential for scientific advance; scientific importance and novelty; and tractability. This last criterion specifically referred to whether the area was sufficiently developed that there was an existing pool of potential PIs that could generate competitive proposals, while still being sufficiently novel and front-line to represent potential for significant scientific advance.

The genomic and molecular genetics oriented initiatives grew out of an appreciation for the rapid advances in both methods and accessibility of molecular approaches and computation related to complex or extensive datasets. Such advances have fueled the development of such areas as genomics and bioinformatics, and population biology is well poised to take full scientific advantage of these developments. Discussion of these areas of research also took into consideration parallel initiatives being generated at NIH and elsewhere in order to promote complementarity rather then competition among agency research programs.

Environmentally oriented research initiatives were developed with consideration for areas of potential societal and applied significance as well as scientific importance. Indeed, an overall theme of this section was that change is an inevitable feature of biological systems and their background environments. Given that humans represent a major agent of environmental change, it is increasingly evident that more scientific emphasis needs to be placed on integrated biotic responses to environmental perturbation as well as human-dominated environments. One of these potential research foci, invasive species, has become the object of an executive order calling for research on the biology of invasive species since the task force meeting. Indeed, a special research initiative in this area was established through the Population Biology Program at NSF in the fall of 1999.

There were also several competing concepts of how to best implement focused research initiatives, including either targeting within existing programs or developing specific new funding initiatives. The model proposed to the group by then Division Director Bruce Hayden was given extensive consideration.

Under Dr. Hayden's model, new initiatives targeting focused research areas such as those defined above would receive separate funding and would be the object of a call for proposals that would be distinct from the usual Panel meetings. The objective would be to allocate approximately \$1.5-2.0 million to such an initiative, with a goal to fund 8-10 projects in that area. Since these areas are perceived to be emerging areas of scientific importance, additional funding would be made available to enable regular meetings among the PIs, creating in effect a collaboratory consortium working individually but with a collective awareness of the overall initiative, to advance the targeted research area.

A successful collaboratory consortium would be reflected not only by the individual and collective scientific accomplishments of the group, but also by the generation of future proposals addressing the targeted scientific area, which would then be part of the overall pool of proposals submitted. Thus, a collaboratory consortium in a specific area would only last as long as a grant cycle, making way for reconsideration of what would then be identified by future task force groups as emergent areas of research.

The recently established bio-wide initiative at NSF, Research Coordination Networks, provides an effective framework for implementing collaboratory groups as described by Dr. Hayden's model. This new program provides opportunities for groups of PIs to define collaboratory groups and apply for funding to support their interactions.

| FRONTIERS IN POPULATION BIOLOGY                    |            |                                  |                                      |  |  |  |
|--|------------|----------------------------------|--------------------------------------|--|--|--|
| Linkages to genomics and molecular genetics        |            | Linkages to environmental issues |                                      |  |  |  |
| Genetic architecture and evolutionary trajectories |            |                                  | Invasive species                     |  |  |  |
| Divergence of genetic architectures                | EVOLVING S | YMBIOSES -                       | Community genetics                   |  |  |  |
| Evolution of complex phenotypes                    |            |                                  | Evolution in human-dominated systems |  |  |  |

# **APPENDICES**

Appendix 1. Proposals reviewed by NSF Population Biology Panels for FY1994-1997:

| CATEGORY                     | TOTAL (more than one category can apply to each proposal) | % OF PROPOSALS<br>REPRESENTED<br>IN TOTAL | AWARDS<br>(more than one<br>category can apply to<br>each proposal) | % of proposals<br>represented in<br>Awards | CATEGORY-SPECIFIC<br>SUCCESS RATE |
|------------------------------|---|---|---|--|-----------------------------------|
| Population Dynamics          | 188   | 26%                                       | 29  | 20%  | 15%                               |
| Population Genetics          | 254   | 35%                                       | 51  | 35%  | 20%                               |
| Life History Studies         | 264   | 36%                                       | 42  | 29%  | 16%                               |
| Molecular Population Studies | 237   | 32%                                       | 44  | 31%  | 19%                               |
| Quantitative Genetics        | 115   | 16%                                       | 32  | 22%  | 28%                               |
| Population Theory            | 69  | 9%  | 17  | 12%  | 25%                               |
| Total (Actual)               | 735   |   | 144   |  | 20%                               |

EXAMPLE: Of the 735 proposals submitted over FY1994-1997, 237 (32%) were coded as Molecular Population Studies. Of the 144 awards made, 44 (31%) were coded this way. Of the 237 proposals coded as Molecular Population Studies, 44 (19%) were successful.

# Notes:

- $1. \ \ Includes \ only \ proposals \ for \ which \ Population \ Biology \ was \ primary \ program$
- 2. Data for this report were taken from Program records and therefore may differ from official National Science Foundation source documents which are generated from the Management Information System database and which may contain different inclusions/exclusions.
- 3. Categories Used in the Population Biology Program

<u>Population Dynamics</u>: analyses of mechanisms affecting the fluctuation, stability, spatial and temporal distribution, abundance and extinction of populations and species, including interactions between species.

<u>Population Genetics</u>: analyses of the Mendelian and non-Mendelian genetic bases of population change and adaptation, including studies of the genetics of life history traits, gene flow, population genetic structure, the roles and maintenance of genetic variability and recombination during evolution, and the genetics of coevolution, hybridization, and speciation.

<u>Life History Studies</u>: analyses of quantitative measurements of the demographic and life history features that are related to the ecological aspects of adaptation in populations and species, and larger phyletic divergences.

<u>Molecular Population Studies</u>: analyses of molecular genetic variation in populations, mechanisms of molecular biological evolution, and diversification of genomic structures and functions in relation to population adaptation and change, macroevolution, and speciation.

Quantitative Genetics: analyses of polygenic inheritance, genetic variances and covariances, and evolution. Includes research on the polygenic basis for the evolution of complex adaptations including coevolution, life history and demographic characteristics, speciation, and phyletic divergences.

<u>Population Theory</u>: mathematical, statistical, computational (simulation) analyses and modeling of population structure, dynamics, adaptation, genetic and ecological diversification, extinction, and speciation.

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