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Cover picture : The Florida panther (bottom left, photo courtesy US Fish and Wildlife Services, see also figure 3), the beaver (top left, see also figure 3), the Bezoar goat (top right, photo courtesy Osman Yöntem) and the Siberian Jay (bottom right, photo courtesy Hannu Siitonen) are all species that have suffered from human impact on nature and as such have become endangered. For instance, the Bezoar goat (wild goat, *Capra aegagrus aegagrus*), here pictured in Termessos National Park (Turkey), is classified by the IUCN as vulnerable as numbers are decreasing mainly because of hunting. The Siberian jay (*Perisoreus infaustus*) is a species which has suffered particularly from the loss and fragmentation of the boreal coniferous forests. At least some of the populations of this species have become highly inbred.

Introduction

Human impact on nature has increased extinction rates of populations and species dramatically and many species are currently on the brink of extinction. Habitat deterioration, fragmentation and destruction are now recognised as a major threat to the persistence of populations and species. Within the field of conservation biology the role of conservation genetics has been greatly emphasised. This role is twofold. On the one hand, conservation genetics provides the tools to study the demographic dynamics of endangered species (e.g. by the use of molecular genetic markers), to infer their past history (identification of bottlenecks and population expansions), to resolve taxonomic uncertainties, and to define management units. On the other hand it studies the consequences of genetic processes that are inevitable in small fragmented populations: genetic drift and inbreeding will cause loss of genetic diversity and an increase in homozygosity. This process of genetic erosion can seriously reduce the adaptive potential of populations to changing and deteriorating environments, can decrease average individual fitness (inbreeding depression) and, consequently, can significantly increase the extinction risk of endangered species.

The emerging field of conservation genetics can significantly contribute to the preservation of nature. Different approaches and methodologies, i.e. theoretical, experimental and applied, are needed to build a consistent framework. The ESF Research Networking Programme on Integrating Population Genetics and Conservation Biology: Merging Theoretical, Experimental and Applied Approaches (ConGen) aims at providing a venue for concerted scientific action in the field of conservation genetics, and to combine and integrate the different perspectives.

The running period of the ConGen Programme is for five years, from November 2004 to November 2009.

Fig. 1: Genetic studies also have an important role in re-introduction and supplementation programmes of wild populations with captive stocks. Studies of captive stocks of the Lesser white-fronted goose (*Anser erythropus*) have revealed several hybridisation events with other geese species, making captive stocks unsuitable for re-introductions.

(Photo courtesy Ingar Jostein Oien)



Background

Human impact on nature

Many plant and animal species currently have to cope with human-induced alterations of their natural environment. Climate is changing globally at a speed that is higher than has been observed in the past 10 000 years and projections into the future show an acceleration of global temperature rise. Chemical pollution and other alterations in the physical habitat have caused the environment to become more and more hostile. In addition, destruction of natural habitats for agricultural development, industrialisation and urbanisation have caused – and still cause – a considerable decline in population numbers and an increase in extinction. Importantly, suitable habitat not only deteriorates but also becomes greatly fragmented, leaving isolated patches of habitat in an otherwise uninhabitable 'desert'. This will certainly impede migration rates and lead to decreased connectivity between populations. Consequently, many (endangered) species find themselves confined to small habitat patches that can sustain only a limited number of individuals. As such, these small populations become increasingly affected by stochastic events, which significantly increase the probability of extinction through random demographic, environmental and genetic forces. It is estimated that a significant proportion of the world's species may become extinct in the next few decades, while many more species are considered to be either endangered or vulnerable to extinction.

Genetics and conservation biology

Conservation biology is the scientific discipline that deals with understanding the forces involved in biodiversity dynamics and provides principles and tools for preserving biodiversity. Within this field conservation genetics deals with (i) the genetic processes that affect the persistence of populations and species, of which genetic erosion is central, and includes development of management measures for minimising the extinction risks related to genetic erosion; (ii) genetics also provides the tools to describe the structure and dynamics of biodiversity at the genetic level, both in the past and at present, and it also provides the tools to study and to infer evolutionary change; and (iii) genetics provides the tools to determine important aspects of the biology of endangered species and to estimate important ecological parameters, e.g. factors concerning the reproductive system of a species, dispersal and migrations patterns. Such data are often crucial to devising adequate management measures. Although in the past there has been some discussion about the relative importance of ecological and genetic processes in relation to the extinction risk of endangered species, it is now well established that these should be studied in concert because genotype-by-environment interaction affect both.

Integrating all these aspects, tools and processes will contribute importantly to understanding the consequences of changing and stressful environments, habitat fragmentation and accompanying genetic erosion for extinction risks and the dynamics of adaptation of species to human-induced alterations of the natural environment, forming the new scientific discipline of conservation genetics.

Scope of the Programme

The founding ideas of conservation genetics in the 1980s concerned the impact of genetic drift and inbreeding on population persistence. Though the issue of genetic erosion has remained central, the field has since then greatly expanded. Broadly speaking, the scientific research currently focuses on two interrelated topics. First, research into the impact of genetic erosion on mean fitness and the extinction risks of endangered species, particularly in relation to changing and deteriorating environments. Second, the value and use of different molecular markers and other tools in characterising (adaptive) diversity, analysing the demographic structure and dynamics of endangered populations, and inferring conservation units. In the end, conservation genetics should be aimed at providing information, tools and guidelines for (genetic) management of small, endangered populations and species. Several important issues that dominate the field of conservation genetics are highlighted below.

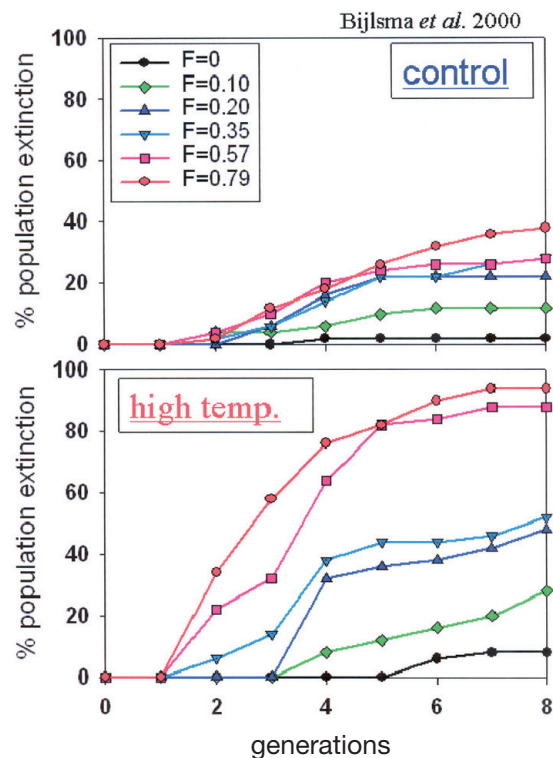
Inbreeding depression and extinction

Genetic erosion in small isolated populations is thought to result in an increase in homozygosity whereby recessive deleterious alleles become expressed causing a decrease of fitness: inbreeding depression. There is little doubt that inbreeding depression can be severe in normally outcrossing species. However, except for some laboratory experiments, it is still difficult to show the direct effects of inbreeding depression on persistence, particularly for natural conditions. For one thing, this may be because the effects under normal conditions are subtle and accumulate slowly and thus may become apparent only in the long term. For another thing, genetic and ecological factors are not independent and are often difficult to disentangle.

Therefore, studies that integrate genetic, environmental and demographic processes are needed. This is the more important because several observations suggest that the consequences of genetic erosion become more pronounced under stress conditions, thereby greatly increasing mortality and extinction probabilities. This synergistic interaction between inbreeding depression and environmental stress is currently poorly understood and based on limited studies. Thus there is a great need to increase and extend those studies also to natural conditions.

Fig. 2: The problems of genetic erosion can be experimentally investigated using *Drosophila* as the model organism. The figures show the percentage extinction of small *Drosophila* populations (30-100 individuals) in relation to the degree of inbreeding (F-value) these populations had experienced prior to the experiment.

The experiment was done under benign conditions (top) and stress, high temperature, conditions (bottom). Clearly, the extinction risk of small populations increases when the level of genetic erosion increases. Importantly, this effect is strongly amplified under stressful conditions. (After Bijlsma et al. (2000) J. Evol. Biol. 13:502).



Scope of the Programme

Purging and the genetic architecture of inbreeding depression

When genetically eroded, there is also considerable variation in the magnitude of inbreeding depression, not only for different life history traits, but also between species. Upon inbreeding, some species seem to suffer greatly from inbreeding depression while others seemingly are unaffected by genetic erosion. In part, this might be due to the fact that species have different life histories and differ in demographic parameters. For another part, it has been suggested that a sufficiently slow rate of inbreeding may enable natural selection to purge deleterious alleles from populations, thereby reducing the impact of inbreeding depression. Much also depends on the genetic architecture underlying inbreeding depression, whether it is caused by a few genes with large or many with a small effect on fitness, by recessive or overdominant alleles, or by epistatic and pleiotropic effects. If we want to predict which species under what conditions will be impacted by inbreeding depression, we need to know much more about the causation of this phenomenon, its timing and how this affects the possibility of purging.

Genetic rescue and outbreeding depression

Migration or gene flow between isolated populations, either naturally or artificially by means of translocation of individuals, may counteract inbreeding depression. This process of 'genetic rescue', however, is not without danger as different populations may be locally adapted to different environmental conditions. Imposing gene flow will then lead to 'hybrids' that are not locally adapted and consequently suffer from outbreeding depression, thereby endangering the persistence of the threatened population even more. It is therefore important to reliably assess the contribution of outcrossing depression to the extinction risk of populations. Information about the degree and scale of local adaptation in metapopulations is therefore a prerequisite.

Fig. 3: Contrasting examples of genetically eroded species that differ greatly in their effects. The Florida panther (*Felis concolor coryi*, top, photo courtesy US Fish and Wildlife Services) population in the Everglades is highly endangered as it has been small for a long time and consequently shows many signs of inbreeding depression (e.g. greatly decreased sterility).

The beaver (*Castor fiber*, bottom) population in Sweden has gone through a severe bottleneck and is based on the level of highly inbred genetic variation. Nevertheless, the population has greatly expanded from less than 50 around 1900 to more than 100 000 currently, indicating that the population shows few problems with inbreeding depression.



Scope of the Programme

Environmental change and adaptive potential

Environmental stress is not only important in relation to its impact on inbreeding depression, but also imposes severe selection. As migration to a more optimal habitat is often not an option due to fragmentation, populations are forced to adapt, either phenotypically or genetically, to the changing environmental conditions. The rate and degree of adaptation strongly depends on the amount and nature of standing genetic variation in a population. Since genetically eroded populations are expected to have lower levels of variation, the adaptive potential may have become greatly limited and thus the extinction risk is increased. As, in contrast to neutral variation, little yet is known on the level, dynamics and nature of adaptive variation in small populations; we need much more information to this end. At the same time we need also to know much more about the role and importance of phenotypic plasticity in this respect.

Genetic markers: neutral versus selected markers

An array of molecular genetic tools are currently available to investigate important characteristics of populations. Neutral genetic markers, such as microsatellites, are widely used to assess inbreeding levels, the level of genetic variation, population structure, the connectivity between populations (gene flow), demographic parameters and phylogenetic or conservation units. In addition, assessment of neutral genetic variation is also informative for inferring ancient or recent historical dynamics of populations. Such data are vital for providing practical solutions, resulting in tools and guidelines for management of endangered species.

However, such neutral data present limitations to measuring variation at loci that are related to fitness and adaptation. Comparing differentiation between populations for neutral markers (F_{st}) to differentiation for fitness-related traits (Q_{st}) may partly mediate this problem. However, the latter measure is also affected by the environmental conditions and may not well reflect genetic differences. Therefore, development of non-neutral marker systems, e.g. SNPs in functional genes, and implementation of modern genomics techniques to study the dynamics of functional genes, to study adaptive processes and to distinguish the consequences of natural selection from that of genetic drift, is of utmost importance.

Fig. 4: Illustration of the use of genetic markers for assessing genetic variation within species. The figure shows the variation at three microsatellite loci (marked green, blue and yellow, respectively; the red bands are the result of a distance marker for reference purposes) in a pine marten (*Martes martes*) population.

Each vertical lane shows the microsatellite pattern of a single individual. Clearly, all three markers are highly variable in this population.

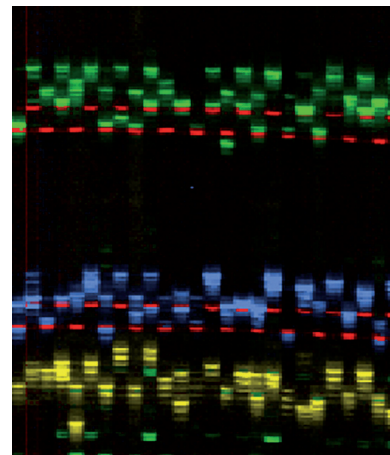


Fig. 5: The pine marten (*Martes martes*) is an endangered species with a highly fragmented population structure in many European countries.

Its genetic structure is currently analysed in order to evaluate its genetic status, to estimate connectivity between (local) populations, and to assess phylogenetic relationships.

Photo courtesy Aksel Bo Madsen.



Scope of the Programme

Theory: modelling approaches and software development

Conceptually, conservation genetics is soundly based on existing population genetic and population ecology theory. However, this 'classical' evolutionary framework was mainly constructed for reasonably large population and equilibrium situations. Unfortunately, in conservation genetics we are dealing with small populations fluctuating greatly in size, where the dynamics is highly stochastic and non-equilibrium situations are the rule rather than the exception: metapopulations in which local populations continuously go extinct and become recolonised will probably never attain an equilibrium situation. Moreover, the complexity and the many interacting processes involved cause convergence to a comparable genetic architecture of populations in time, even though the underlying demographic and genetic processes differ fundamentally.

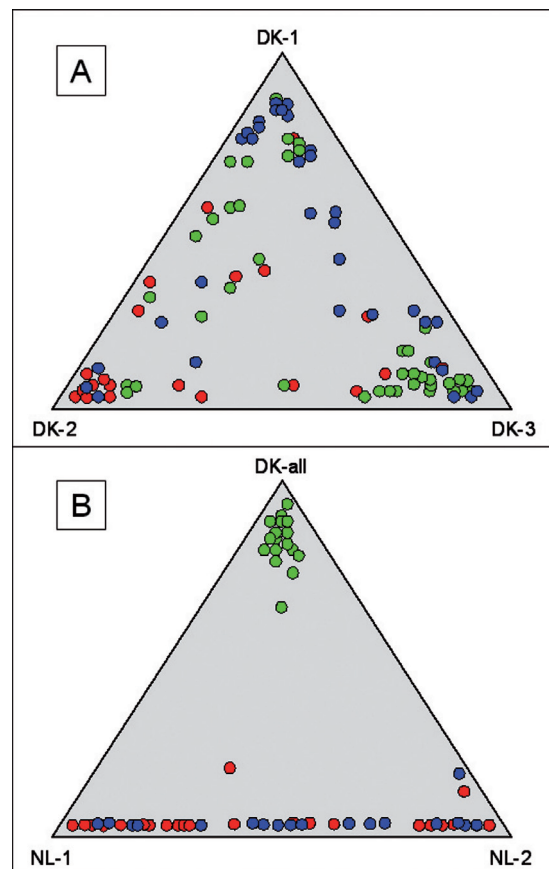
Consequently, there is a great need to extend and adapt existing theory and to develop new theoretical models that will be tailored to such a highly dynamic situation. To this end, individually based simulation models show great promise in combining genetic and ecological theory and may revolutionise conservation genetic theory. Such models have to be evaluated and validated for their biological relevance in experiments using model organisms and ultimately have to be validated in a natural setting. In addition, also the development of new software that combines new estimation and decision procedures integrating genetic ecological and environmental data is crucial.

Fig. 6: Example of the use of computer software to analyse the population structure and migration patterns of endangered species using multilocus microsatellite fingerprinting whereby individuals are clustered according to their genotypes. The top figure shows the result for three samples from different badger (*Meles meles*) populations in Denmark coloured according to their sample location (DK-1: blue; DK-2: red; DK-3: green).

The individuals of the three populations in the majority are assigned to different clusters in the corners of the triangle, indicating genetic differentiation between populations. However, some individuals sampled in one population cluster genetically with another population (blue individuals in the bottom corners) and can be regarded as migrants from DK-1. Individuals along the side of the triangles can be interpreted as offspring of migrants that share genetic information of two populations.

The bottom figure shows the result of the same exercise for samples of two Dutch badger populations (marked blue and red, respectively) combined with Danish badgers (marked green). In this case the Danish badgers cluster in the top corner, while the Dutch individuals all are located along the basis of the triangle.

This indicates that Dutch and Danish badgers are clearly differentiated and totally isolated, whereas the two clusters postulated within the Netherlands seem well connected by migration. (Data Van de Zande et al (2007) *J. Zool.*, in press).



Aims and Objectives

All the problems mentioned above are strongly interrelated and necessarily have to be approached from different perspectives, requiring concerted action of the different sub-disciplines in conservation genetics. As such, the Programme on Conservation Genetics (ConGen) aims to promote:

(i) the development of theoretical models that will strengthen the conceptual basis of conservation genetics and allow better and more rigorous predictions and provide a framework for designing critical experiments, for decisively analysing empirical data, and for reliably developing guidelines for management.

(ii) the design and execution of critical experiments, both in the laboratory and under natural conditions, that, on the one hand, evaluate and test the predictions from theory in a biological context and parameterise predictive models, on the other hand, disentangle and deconfound the effects of the different underlying processes and causes involved.

(iii) the translation of the insights gained by the conceptual and experimental approaches into schemes, tools and guidelines for the natural and applied situation to provide practical solutions for the management of small endangered populations.

Integration of experimental, theoretical and applied conservation genetics will certainly have strong synergistic effects and will contribute significantly to improving our understanding of methodological and applied aspects of conservation genetics. In this way, we not only may come to a better understanding of threats that await biodiversity, but it will also allow us to devise better (management) measures to overcome the problems. ConGen will provide an excellent platform for this.

The central objective of the Programme on Conservation Genetics is to combine and integrate the different research areas involved in the field and to merge European efforts and expertise to reach a critical mass of teams to lead the field worldwide. The synergy resulting from such an integration of scientific knowledge, methodological toolboxes and data will not only lead to better insights into conservation genetic issues but also provide crucial information for European policies on conservation of biodiversity, e.g. in relation to global change and European-wide nature conservation efforts. Many of the questions addressed in ConGen are questions currently addressed in general evolutionary biology. Therefore, the merit of the programme is not restricted to conservation genetics but is also expected to generate important scientific spin-off relevant for the whole field of evolutionary biology.

Programme Activities

During its five year running period the programme will:

- a) educate and train young scientist in interdisciplinary and collaborative research in the complex field of conservation genetics;
- b) review and standardise research approaches and evaluation procedures across Europe;
- c) facilitate the implementation and development of new and recent molecular and theoretical tools;
- d) detect and evaluate new developments in the field of conservation genetics and effectively disseminate the implications to the European scientific community and make these accessible to other social actors such as nature managers and policy makers;
- e) to establish a scientific network facilitating access to, and exchange of, sample material of endangered species across Europe.

These objectives will be pursued by carrying on the following activities:

- 1) Training (courses and exchange visits)
- 2) Workshop and conference organisation
- 3) Communication and interactions with other programmes

Funding

ESF Research Networking Programmes are principally funded by the Foundation's Member Organisations on an à la carte basis. ConGen is supported by:

- Fonds zur Förderung der wissenschaftlichen Forschung (FWF)
Austrian Science Fund, Austria
- Fonds voor Wetenschappelijk Onderzoek (FWO)
Fund for Scientific Research – Flanders, Belgium
- Hrvatska akademija znanosti i umjetnosti (HAZU)
Croatian Academy of Sciences and Arts, Croatia
- Akademie ved České republiky (AVČR)
Academy of Sciences of the Czech Republic, Czech Republic
- Grantová agentura České republiky (GAČR)
Grant Agency of the Czech Republic, Czech Republic
- Forskningsrådet for Natur og Univers (FNU)
Natural Science Research Council, Denmark
- Finlands Akademi (AKA)
Academy of Finland, Finland
- Centre National de la Recherche Scientifique (CNRS)
National Centre for Scientific Research, France
- Országos Tudományos Kutatási Alapprogrammok (OTKA)
Hungarian Scientific Research Fund, Hungary
- Magyar Tudományos Akadémia (MTA)
Hungarian Academy of Sciences, Hungary
- Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO)
Netherlands Organisation for Scientific Research, Netherlands
- Norges Forskningsråd (NFR)
Research Council of Norway, Norway
- Comisión Interministerial de Ciencia y Tecnología (CICYT)
Interministerial Committee on Science and Technology, Spain
- Consejo Superior de Investigaciones Científicas (CSIC)
Council for Scientific Research, Spain
- Vetenskapsrådet (VR)
Swedish Research Council, Sweden
- Türkiye Bilimsel ve Teknolojik Arastırma Kurumu (TÜBİTAK)
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