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Proceedings of a Conservation Genetics workshop held at the Royal Botanic Gardens, Kew, 27 November 2001

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Barbara Jones and Ian Taylor

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Dedication

It is with a sense of great sadness that we dedicate this volume to the memory of Bill Havers, who died in June 2002. He will be remembered as a great conservationist and, in particular, as the Chairman of the Chiltern Military Orchid Group. Until the end of winter 2001/02, he was active at Homefield Wood working on a new clearing. He attended this Conservation Genetics Workshop and provided thought provoking and, at times, challenging input to discussions, always in his good-humoured way. He is remembered with great warmth.

Acknowledgements

We would like to express our thanks to the people who helped with the organisation of this meeting – without this help the meeting would not have been possible:

Robyn Cowan, Ruth Davies, Andy Jackson, Lola Lledó, Olivier Maurin, Vivien Munday, Mark Raven and Chris Sydes.

And to Mary Roberts of English Nature who checked the transcript.

Introduction to the UK Plant Conservation Genetics Workshop

Jill Sutcliffe, Botanical Manager, English Nature

In the summer of 2000, members of the country agency staff who concentrate on botanical issues agreed that it would be useful to hold a genetics and conservation workshop. Initially when genetic techniques were being developed there was scepticism about their relevance to conservation issues. Now that useful results are appearing, it was felt it would be timely to hold a workshop and explore some key issues.

The aim of the meeting was to examine the practical outputs of benefit to the conservation of plants. Country agency staff approached the genetics laboratory at Kew and set up a small steering group to think about the content and format of the workshop, and the people to invite. It was decided to keep the workshop fairly small – 50 to 60 people – to allow time for discussion and to focus on getting as many of the institutions and organisations to attend who are engaged with these issues.

Many of the issues facing nature conservation are multidisciplinary and many of the solutions turn out to be interdisciplinary. While the language, techniques and issues used in genetics research are commonplace to those working in the field, they are not familiar to many of the conservationists for whom genetics is but one possible strand in their work.

The conservation staff wanted to find out:

- a basic understanding of the issues raised by genetics research;
- the techniques and their limitations;
- the right questions to be asking.

The genetics researchers wanted to find out

- what it was the conservationists wanted to know;
- how their work might be of relevance to conservationists;
- how to tease out issues affecting conservation in their reports having done the work in the lab.

The workshop was designed to cover these issues in three sessions and the main recommendations are summarised below:

Main workshop recommendations

- A database of conservation related genetics research should be established for web access by all. A prototype is being established at Leicester and the possibility of extending this will be investigated during the first meeting of the inter-agency/research group

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- Increase levels of collaboration between researchers and conservation agencies. To this end the workshop considered the establishment of an inter-agency group to include an equal number of researchers to progress items such as the database. Representation on the group would be relatively constant from the agencies but researcher representation could change according to the issues being discussed. The group could also become a focus for investigating the establishment and funding of large scale (European) initiatives.

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- Advice is needed on situations and taxa requiring work. Most conservation staff will generally not read scientific papers reporting genetics research and have little time to look into texts describing genetic issues and techniques. A leaflet or series of leaflets outlining the main situations where some genetics research may benefit conservation decisions and management, and why, would be useful in making more people aware of the potential of such work. This could be pursued by the group described above.

- Researchers would be advised to publicise the results of conservation related research in non-technical journals and publications, such as *Biodiversity News, Conservation Land Management*, *British Wildlife, Plant Talk* and *the National Trust* magazine which are widely read by conservationists. Non-technical descriptions of genetic research on species of conservation concern would again be a good way of targetting an important audience.

Contents

Introduction and context for the day

It was a great pleasure to host this meeting at the Royal Botanic Gardens and particularly in the Jodrell Laboratory. It is appropriate that the Conservation Genetics Workshop was held in this building, given the long-standing nature of the Jodrell's active interest in some of Britain's rarest plants.

When I took up the post of Keeper in 1987, I was almost immediately involved in this area of work – specifically related to the lady's slipper orchid, *Cypripedium calceolus*. The genetics of this species and its relationship to other species of slipper orchids formed part of the PhD of Tony Cox. Using the techniques available at that time, his study of infraspecific variation did not yield conclusive results, and despite the advent of more sophisticated techniques in the 1990s, this species continued to prove intractable as a result of the large genome size, the subject of my own personal research for many years. However, I am happy to say that we have persevered with the lady's slipper orchid, and a recent paper published from the Jodrell (Fay & Cowan, 2001) describes the development of a new set of genetic markers which are finally allowing us to address the genetic questions relating to this species.

With the launching of the Species Recovery Programme by English Nature in 1991, Kew's activities have continued to be linked closely to the aims of the conservation agencies, not only in terms of genetics, but also in micropropagation and seed banking. The formation of the Molecular Systematics Section in the early 1990s followed by the Conservation Genetics Section more recently show Kew's active response to the developing field of molecular biology and the challenges associated with the application of the techniques to conservation-related questions.

Kew greatly values our joint work with the conservation agencies and other colleagues in this important area, turning laboratory science into management recommendations that are then applied in situ. We hope that these relationships will continue to prosper in the years to come.

It was good to see such a broad mix of conservation practitioners and lab scientists talking together, and I believe that this was a constructive, informative and enjoyable day for all concerned.

Professor Mike Bennett
Keeper, Jodrell Laboratory

Reference

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Session one: Background

The state of genetic knowledge of the British Flora

Pete Hollingsworth, Royal Botanic Garden Edinburgh

The British Flora is exceedingly well characterised compared to other floras. It consists of some 1407 native species (excluding microspecies), 1204 introduced species, and 785 hybrids (data source BRC Monks Wood). The flora has benefited from two large-scale mapping exercises, the development of the Biological Records Centre database (9.05 million records), the production of National Floras, a Vice-committal Flora, local county floras, the BSBI literature database (containing ca 32K records), the Red-data book and Scarce Plants Atlas, the Threatened Plants Database and numerous Biological Floras and ecological accounts. A chromosome database of the British flora at the University of Leicester contains 8151 records with localised chromosome counts based on native material of 77% of the British flora.

The situation with regards to population genetic information is less clear cut - there is no central repository for this information. Estimates based on a literature review by Quentin Kay (University of Wales), coupled with estimates on unpublished data from three Edinburgh-based population genetics groups extrapolated to a national level, suggest that there is some sort of genetic data on about 10% of the species in the flora. Bearing in mind that the British flora is not very species rich, its flora is genetically well known compared to other countries, and the Species Action Plan species are relatively well covered (ca 45 % of vascular plant species on the BAP ‘short-list’ are taxonomically controversial but molecular data is available or research underway on 90% of these). However, there is still no information on about 90% of the species in the UK vascular plant flora, and virtually no data at all on groups such as bryophytes and lichens.

It should also be stressed that genetic data are gathered for many different purposes, and information gathered for one type of study, will not necessarily be transferable to another. Key areas where data are being gathered include: species delimitation, hybridisation, phylogeography, broad scale population structure, and reproductive ecology (including breeding systems estimates, direct measures of gene flow and comparative assessments of sexual versus asexual reproduction). Information from these separate biological questions often requires different sampling regimes of both genes and individuals.

Three recommendations were made from this overview of the state of knowledge of the flora.

Richard Gornall's (University of Leicester) plan for a Genetical Flora of the British Isles should be pursued with some urgency. Capturing this information and placing it in an accessible format would provide an exceedingly valuable resource. The database should be designed to allow future user-submission.

There is a current focus on genetic studies on the very rare. It is likely that we will learn more about genetic resources and conservation biology in looking at more common species, and declining scarce species, than we will from examining the genetics of small impoverished populations.

Genetic data in an ecological vacuum is of limited value. A stronger integration of data from neutral genetic markers with ecological information (eg fitness/adaptation, demography, landscape context of populations, herbivores/pathogens/mutualists) will increase the biological value of the data.

Genetic tools for conservation

Richard M Bateman and Johannes C Vogel, Department of Botany, Natural History Museum, London

Need for population genetic data

Any effective integrated approach to species conservation requires the comparison and comprehension of sound data on ecology, demographics, morphology and molecular genetics.

Uses of genetic markers

Uses of markers in population genetics include: estimating genetic diversity and differentiation within populations; estimating rates of gene flow and organismal migration within and between populations; characterising mating systems; analysing parentage and maternity/paternity. Immediate benefits to other research disciplines include: delimiting species and infraspecific taxa; reconstructing phylogeny (both for systematics); developing genetic linkage maps and quantitative trait loci (QTL: evolutionary-developmental genetics).

Main classes of genetic markers

There are three main classes of genetic markers: morphological (= classical: not considered further here); biochemical (eg isozymes, organic biochemicals); DNA-based markers (eg sequencing, ISSR microsatellites, Amplified Fragment Length Polymorphism).

(a) Isozymes

Established in the early 1970s, isozymes are universally applicable and well-established. They yield abundant comparative data and constraints on their use are now well understood. They are co-dominant markers representing up to 20–30 Mendelian loci, and allow comparison up to genus level. It is a good all-round technique for most questions, including detection of polyploidy, but it is not always adequate for studies of fine-scale gene-flow, paternity or spatial structure.

(b) Randomly Amplified Polymorphic DNAs (RAPDs)

This was the first DNA-based technique to be widely used, and can be applied without much preparative work. It is a dominant marker system offering an almost unlimited number of loci, and thus offers a useful test for clonal reproduction. However, results have proved difficult to reproduce, both within and between laboratories, and it is difficult to make inter-specific comparisons. Thus, this technique has in recent years largely been replaced by AFLP and microsatellite approaches.

(c) Amplified Fragment Length Polymorphism (AFLPs)

This more recently developed and increasingly widely used marker system offers an almost unlimited number of dominant loci in a single assay and is increasingly automated, but it does require protocols to be developed for each problem addressed. Comparison has proved difficult between distantly related species within a genus, and problems of reproducibility and band homology determination are still emerging.

(d) Microsatellites

These relatively recently developed co-dominant markers represent a limited number of loci with unusually high degrees of polymorphism. Like AFLPs, these are increasingly automated and multiplexed, but they still require a complex and often very time-consuming protocol development for each project. They are more effective for studies of fine-scale gene flow, maternity and spatial structure than for large-scale species comparison.

(e) Organelle DNA

Plastids and mitochondria undergo predominantly uniparental (usually maternal) inheritance, and are most effective for studies of population structure and, when combined with nuclear markers, estimating pollen to seed-flow estimates and identifying hybrids.

The most common approaches are: Random Fragment Length Polymorphisms via the polymerase chain reaction (PCR-RFLP), which allow broad-scale genetic structure and population surveys but may be insufficiently variable at local scales, and; chloroplast microsatellites, which allow general population surveys but can be too variable at broader scales, incurring unacceptable levels of homoplasies that are not readily identified.

Choosing the best marker system(s)

The most useful criteria for comparing marker systems are: number of loci and degree of polymorphism; dominance and null alleles, transferability of loci among taxa; reliability and reproducibility; ease of assay; opportunities for automation and multiplexing; and costs in both consumables and staff time, including the time needed to effectively establish the necessary protocols for the question at hand (eg Glaubitz & Moran 2000).

On average, studies requiring large numbers of loci are best conducted using AFLPs (or RFLPs), those requiring high discriminatory power by microsatellites and those requiring species-level phylogeny construction using direct sequencing techniques. Isozymes remain a cheap, straightforward technique for initial surveys, but their usage (at least, in botanical studies) decreased rapidly following the appearance of PCR-based techniques in the early 1990s, falling from almost 100% in 1991 to *ca* 50% by 1997 and perhaps 20% today.

Key conceptual issues

The benefits to conservation of population genetic data directly reflect the quality of the conceptual context in which they are analysed, not least developing the most appropriate theoretical models. Issues such as inbreeding depression and genetic load still carry considerable controversy regarding the frequency and profundity of their effects in natural and semi-natural communities, yet there remains in conservation biology a simplistic refrain of "high diversity good, low diversity bad". Remedial work against low diversity can be very costly, and therefore requires a more carefully considered approach. Key questions for further discussion include:

How strong is the evidence that low genetic diversity is detrimental to a plant population? And under what circumstances is it most likely to be detrimental?

How easily can detrimental, neutral and adaptive alleles be distinguished? And how easily can an allele switch between categories? (cf. Hedrick 2001)

What is the most appropriate geographical scale to study natural genetic variation? And do we yet know sufficient about genetic variation in common species, as opposed to the rare species that are the focus of conservation bodies?

How can we best translate population genetic data into specific/infraspecific taxonomies? And do we know sufficient about correlated morphological variation to optimally interpret population genetic data?

Conclusions

(1) The UK possesses a broad base of well-equipped laboratories and skilled scientists able to conduct all relevant techniques and to analyse the resulting data.

(2) The UK has unrivalled natural history collections, a species-poor (and thus manageable) biota as a result of the Quaternary glaciations, and an exceptional knowledge of the morphology and ecology of that biota provided over the last three centuries by both professional and amateur natural historians.

(3) However, the increasingly sophisticated techniques available to conservation biologists are only as effective as the quality of the scientific questions asked and our understanding of the biological context in which the results are interpreted.

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Session Two: Genetics issues

Conservation genetics and its relevance to conservationists

Barbara Jones, Countryside Council for Wales

For many conservation managers the most important issues in their work are to halt the loss and fragmentation of habitats and species and to restore the condition of remaining fragments of semi-natural vegetation. Priorities for plant conservation revolve around species considered to be under the greatest threat based on demographic and distribution data. Genetic factors are marginal and rarely considered, indeed they are often deemed to be irrelevant to their work and a luxury only to be afforded if there is the time, resources and interest in a particular organism to commission such research, or if overriding genetic considerations are proven. Many of the topics considered by geneticists to be important – for example, gene flow, evolutionary history, quantitative variation for adaptive traits, fitness and genetic structure, do not even have names in conservation discussions, where the main concerns usually just revolve around the size of the population, the number of flowering plants and whether the population/species is decreasing or not.

Because there is so much to do in conservation with so many large-scale concerns and few resources, for genetics to become relevant to conservationists, there is a need to focus on practical questions and issues which conservation bodies have asked, or are likely to ask, remembering at the same time, that often conservationists do not know which questions to ask or even whether there is a question at all! Genetics is another world to many practicing conservationists and the barriers need to be broken down to show that genetics studies/research can answer some real conservation questions and facilitate species management.

Conservationists want answers to questions with direct conservation applications, eg information on how to manage a species to ensure that it does not become extinct in a particular location, to increase the size of the population and to improve its chances of adapting to future environmental change. Any research relating to conservation genetics should therefore use conservation language and, if appropriate, be related to (cost effective) management. There are a number of issues and questions conservationists are likely to be concerned about in genetic aspects of species conservation. These include:

- When does genetics become a factor in the conservation of a species and conversely when does it cease to be a factor in species conservation?
- Small/edge-of-range population viability and future persistence under environmental change.
- Amount of variability – is it important for adaptability and long term survival?
- The taxonomic status of a species, including taxonomic debates. Is it a sub-species, native, endemic?
- Currently evolving genera – how to conserve a ‘species’ - should we be looking at process and habitat management to improve conditions for a species.
- Effects of habitat fragmentation.

- How many populations need to be retained to ensure the species, and its gene pool, is conserved?
- Recovery/restoration situations – when is it advisable to (re)introduce species and what is the best way of going about this?
- Inbreeding/outbreeding scenarios – how to avoid. Is selfing a problem in specific small populations?
- If collections of material for ex situ conservation are needed, what is required?
- How to develop habitat management to improve the demographic and genetic performance of a species.
- Relatedness of a species/population to its closest relatives (evolutionary history).
- When do genetic factors of a species or population become so critical and override environmental factors, that, if not taken into consideration and managed properly, the species/population can become extinct?

One or more of these questions may be relevant to any one particular case, but they all have practical applications and should form the core of what researchers investigate in conservation genetics related research. The following four talks outline some of these issues such as evolutionary history, fitness and gene flow as related to species adaptation and persistence, taxonomic problems, national versus global rarity and the genetics behind (re)introductions and augmentation. Other issues are highlighted in the case studies of recent or ongoing research on *Woodsia ilvensis*, *Euphrasia spp*. and *Orchis militaris*.

Taxonomy, hybridisation and processes

Michael F Fay, Royal Botanic Gardens, Kew

Several groups of plants in the UK flora are good examples of the role of hybridisation in the formation of new species. These groups are among the mostly vexing from a taxonomic point of view, and the conservation of process may be as relevant (or more so) than the conservation of named, but possibly relatively transitory, taxa of hybrid origin.

Dactylorhiza (Orchidaceae) is represented by three diploid lineages (*D. fuchsii*, *D. incarnata s.l.* and *D. viridis* [*Coeloglossum viride*]). In addition, there is one autotetraploid (*D. maculata*, thought to be derived from a diploid species in the *D. fuchsii* lineage) and a range of allotetraploids derived from hybridisation between *D. fuchsii* and *D. incarnata s.l.* or *D. maculata* and *D. incarnata s.l.* Some authors treat the allotetraploids as a single named taxon, *D. majalis* (or *D. elata*), whereas others recognise a variable number of taxa in the group, varying in morphology and ecology (*D. traunsteineri*, *D. lapponica*, *D. purpurella*, *D. praetermissa* etc.). Further complications have arisen as the result of genetic data that demonstrate that some (probably all) of the named allotetraploids have been formed from the parental lineages multiple times, and plants with consistent morphology and ecology do not form coherent genetic groups (eg plants named *D. traunsteineri* are often more closely related to other allotetraploids in the same region than they are to *D. traunsteineri* from other regions; Hedrén *et al.*, 2001).

If we choose to recognise the narrowly named taxa, we increase the conservation burden (several are rare) but do not recognise the biological complexity of the situation. If we recognise only more broadly circumscribed taxa, then we could potentially risk losing locally adapted lineages. In the case of *Dactylorhiza*, it has been suggested by Hedrén (2001) that highest priority should be given to preserving the parental lineages, particularly where these show greater diversity in southern Europe. Conservation of habitats where the allotetraploids flourish in the British Isles and elsewhere would then allow this dynamic process to continue. The patterns occurring in the allotetraploids are being further characterised in ongoing genetic studies (Hedrén 2003; Shipunov *et al.*, submitted, Pillon *et al.*, in prep.). These studies should allow the identification of lineages functioning as evolutionary significant units (EMUs) and those that should be recognised as management units (MUs) as defined by Moritz (1996) to be identified, thus aiding the decision making process relating to the conservation of these plants and allowing us to make recommendations about the number of named taxa to be recognised.

Sorbus presents a different set of questions and problems. Like *Dactylorhiza*, *Sorbus* is represented in the British Isles by diploids (*S. aria*, *S. aucuparia*, *S. torminalis* and *S. domestica*) and allopolyploids (triploids and tetraploids). The polyploids fall in several distinct groups derived from a) *S. aria* (the *aria* aggregate, eg *S. rupicola* and *S. porrigentiformis*), b) hybridisation between *S. aria* and *S. torminalis* (the *latifolia* aggregate, eg *S. bristoliensis* and *S. devoniensis*) and c) hybridisation between *S. aria* and *S. aucuparia* (the *anglica* aggregate, eg *S. arranensis* and *S. minima*). While the diploids are relatively common and not of major conservation significance, many of the named polyploids are extremely rare and several are local endemics in 'hotspots' in western Britain (eg the Avon Gorge, the Brecon Beacons, Morecambe Bay and Arran). Unlike *Dactylorhiza*, the polyploids in *Sorbus* are apomictic (or predominantly so), and once formed they represent genetically stable lineages that no longer (or only rarely) interact with other lineages. As a result, they generally stable in their morphology, making them easily recognisable in many cases. However, named taxa in each of the aggregates are thought to have the same parental species, and some authors question the necessity to recognise multiple taxa in each of the aggregates. Conversely, other authors prefer to recognise yet more taxa for local and apparently distinct forms (eg in *S. porrigentiformis*). We are currently studying the genetics of these taxa (Fay *et al.*, 2001; Chester *et al.* and Cowan *et al.*, in prep.), and these studies will allow us to investigate the parental lineages giving rise to each of the polyploids and to assess the number of times each polyploid has formed. Related studies will also attempt to address questions relating to the occurrence of the 'hotspots'. Together, these types of studies will provide information that can be incorporated into conservation management policies for these species.

Dactylorhiza and *Sorbus* are only two examples in which hybridisation plays or has played an important role in the origin of the taxa we observe today. Other genera include *Betula*, *Orchis* (see later abstract in this volume), *Populus*, *Quercus*, *Salix* and *Ulmus*. Studies of these dynamic situations are not only of scientific interest but also provide information of great use to the conservation of the taxa involved.

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Patterns of genetic variation in the British and Irish flora: The effects of time, chance, change and isolation.

Quentin O N Kay, University of Wales, Swansea and National Botanic Garden of Wales

Harold Macmillan's reply, on being asked what had prompted his actions as British Prime Minister, was "Events, dear boy, events". Events - often chance (stochastic) events, especially during the period from the Late-glacial up to the present - and the properties of the plant populations that they affected, are also responsible for the present composition of the British and Irish flora, and for the patterns of genetic variation in its plant populations.

The effects of these events - climatic change, geographic change, ecological change, habitat fragmentation, and the processes of migration and dispersal – on the distribution and genetic structure of plant populations depend upon the properties of those populations, especially their breeding system and reproductive strategy. For each of these, there is a range of possibilities – 'choices' – with different implications for genetic structure. For the breeding system, possibilities from strict allogamy through a range of intermediate states to strict autogamy, or partial or complete apomixis. For reproductive and seed or vegetative propagule dispersal strategies, the 'choices' can be summarised as stay at home or travel? Quality or quantity? Targeted or broadcast? The distribution of suitable habitat, the mode of arrival of colonising individuals or groups, and the overall pattern of spread (broad front or leapfrogging) interact with these and other factors to produce a wide range of different possible outcomes.

Different habitat-groups of plants have had very different experiences in Britain and Ireland since the Late-glacial. Arctic-alpines, once in many cases widespread, have long been reduced by climatic change to mountain fastnesses, often in small and isolated but long-persistent surviving populations. Plants of open habitats and grassland have had a switchback ride with diverse outcomes, often with drastic recent reduction and threat. Forest species showed a dignified progress to the forest maximum of the Boreal and Atlantic periods but have been reduced to increasingly isolated and artificial fragments by the spread of agriculture and urbanisation. In contrast, strand-line and maritime plant populations probably persist much as they always did, now increasingly with ventures inland, for example to motorway verges. Weeds, aliens and colonists have taken advantage of the spread of agriculture and urbanisation, sometimes with spectacular success at least in the short term, as have some aquatic plants.

Do the patterns of variation of British and Irish plant populations reflect their diverse histories? In the great majority of cases, if only we knew! Although quick and effective molecular techniques for the determination of intraspecific patterns of genetic variation in plants have existed for more than 20 years, and knowledge of these patterns is an essential requirement for any scientifically based species or habitat conservation project, very few studies have been made in Britain and Ireland. Furthermore, as elsewhere, these have been largely confined to a few groups of plants – trees, rare plants, aquatics, invasive species and arctic-alpines. These studies, for example of *Draba aizoides*, *Ononis reclinata*, *Mibora minima*, *Saxifraga oppositifolia*, *S. rivularis*, *Fallopia japonica*, *Vicia orobus*, *Primula scotica* and *Spartina anglica*, have been enormously informative and underline the need for much more work.

Genetics in plant conservation: fitness and gene flow

Richard Ennos, University of Edinburgh

Fitness is an attribute of a genotype or a population of genotypes. It is defined as the ability to leave descendants in subsequent generations relative to some other genotype or population of genotypes. Differences in fitness of genotypes may arise at any stage of the life cycle from seed survival through to reproduction. Fitness is important in conservation because it a major determinant of the ability of a population of genotypes to maintain itself. A fundamental property of fitness is that its value depends on the environment in which it is measured. This is admirably demonstrated by numerous reciprocal transplant experiments. Fitness is usually greatest in the home environment where the genotype has evolved.

There are a number of processes that may lead to a reduction in fitness. The first involves a sudden reduction in effective population size either through a catastrophic event, or through the cessation of gene flow in meta-populations. In the short term existing recessive deleterious alleles are expressed leading to inbreeding depression. Over the longer term newly arising deleterious mutations may become fixed (mutational meltdown). Both decrease the fitness of individuals. Also over the long term genetic variation is lost and is held at a lower equilibrium level than in a large population. The ability of the population to respond adaptively to changes in environmental conditions is therefore reduced.

The second cause of reduction in fitness is migration of maladaptive genes via pollen into a population. The resulting reduction in fitness caused by production of maladapted offspring is referred to as the ‘migrational load’. The third factor responsible for a reduction in fitness is a change in the environmental conditions. The environmental change experienced by an existing population may be abiotic (eg global warming) or biotic (eg movement of a novel pathogen into the region). The consequence of the environmental change may be elimination of the population, or adaptation of the population to the new environment and restoration of adequate fitness. The latter response requires adequate levels of appropriate genetic variation.

Another situation in which environmental change causes reduction in fitness is where populations are deliberately transferred to a new environment, typically during a habitat restoration programme. If the environments are too disparate the population is usually eliminated. However where the population is able to reproduce sexually and has appropriate genetic variation, natural selection will refine adaptation and lead to an increase in fitness in the new environment.

Genetic markers may often be useful in recognising situations where there is potential for a reduction in fitness of a population. By monitoring genetic diversity levels over time it is possible to detect significant loss of genetic diversity associated with fitness reduction. Comparison of gene diversity levels among extant population may pinpoint certain populations with lower marker diversity that are most likely to be suffering from reduction in fitness. Finally genetic markers can be used to measure the extent of gene flow among populations. In fragmented populations this can establish whether fragments are genetically isolated and therefore vulnerable to loss of fitness. In situations where adjacent populations are adapted to different environments, measures of gene exchange can help to quantify the migrational load.

A number of conservation actions may help to maintain and enhance fitness in plant populations. Where population size is very small, supplementing populations with unrelated but adapted genotypes should be considered. Where gene flow has ceased between population fragments, corridors or stepping stone populations can be established to restore gene flow. Finally, when undertaking restoration work, reduction in fitness can be avoided by using material that is adapted to the most similar environmental conditions.

Local adaptation – conservation priorities and the role of conservation genetics

Fred Rumsey, Department of Botany, The Natural History Museum, London

The flora of the British Isles provides a marvellous scientific resource, its patterns of genetic diversity, largely as yet unread, outlining a traceable history of immigration, adaptation and extinction. As a result of an almost complete glacial coverage within the last 15,000 years the vast majority of the elements of the British flora are comparatively young, derived from refugial areas elsewhere, or latterly introduced deliberately, or unwittingly, by man. "Native" status has been a critical factor as to whether a species is deemed conservation worthy, but is rather arbitrarily defined, difficult to prove/disprove and some would argue is just a semantic exercise of little biological or practical merit. It fails to recognise the dynamic nature of our flora and I feel should not be the over-riding criterion for conservation attention.

The recency of our flora has resulted in a very low level of endemism and has favoured those species which disperse and colonise well – factors often linked to breeding system, itself closely correlated to genetic structure. Conservation efforts have traditionally been prioritised towards endemic taxa, although it seems to generate any interest/support these must be of species status – another controversial area dictated by definitions that no two people can agree on. As more and more powerful molecular techniques are employed, all too often we are being forced to realise that the currency of our conservation world "the species" is an artificial construct which just happens to work most of the time.

The question as to where our conservation priorities should lay has long been contested – Do we invest in globally uncommon species which may be relatively abundant in the British Isles, eg. *Hymenophyllum wilsonii* and *Hyacinthoides non-scripta*, which require actions at the habitat/landscape scale (difficult/more costly!) or do we concentrate on national rarities which may be more abundant elsewhere, eg. *Cypripedium calceolus, Saxifraga cernua, Gladiolus illyricus*, etc., etc. Conservation authorities have generally taken the latter approach, with priorities largely decided by abundance on a UK national basis. This approach has been criticised for its parochiality and the fear is that with devolution of the countryside agencies this tendency will only be exacerbated.

The focus on range edge rarities does have relevance but two main considerations should be met, the first purely practical:

1. Is long term in situ survival feasible, given realistic levels of expenditure and staff time (an issue which will assume greater importance, for example as climate change makes the growth of some arctic-alpines untenable)?

2. Do the British populations have unique features which warrant their preservation?

(The question which then leads from this as to when a difference becomes important pragmatically has to be determined by the resources available). Unique features may be readily observed if morphological but if genetic will require in-depth study, the results of which are not predictable a priori. For such studies to be valid they must encompass material from elsewhere in the species range to establish context and allow us to assign levels of significance to any distinctions discovered. Too many conservation genetic reports suffer from their lack of sampling breadth, content perhaps being dictated by inadequate funding and tight deadlines when finding satisfactory answers to well defined biological questions should be the driver.

With the UK BAP process our conservation priorities are being re-addressed and it is to be hoped that biological considerations will assume greater importance when lists are revised; ie threat should be given greater weight than absolute number. Species are rare for different reasons and in different ways. Many absolute rarities are adapted to low population size and accordingly are less threatened than the taxon which still has vastly more individuals but which has declined to a point whereby it may no longer be viable by virtue of its particular genetic characteristics. Informed opinion for selection may require genetic study to assess the importance of fragmentation, population size, etc. but any such studies should seek to address our general lack of knowledge and not concentrate just on rarities. We need to establish the bigger picture before we can make informed judgements about the exceptional.

Understanding a taxon's genetics can be crucial but we must first understand its ecology/biology to ask the appropriate questions and interpret the results. The molecular methods routinely used provide a random (we assume with little justification!) snapshot of variation from throughout the genome. Where we can identify the function of the markers we are looking at – as with allozymes, we assume that these variants are adaptively neutral. Much can be indirectly inferred from these genetic markers in terms of gene-flow, breeding system and as one measure of similarity but they do not provide an assessment of a plants adaptive potential, ie variation in the adaptive characters which may be of more practical concern. Selective breeding studies and common garden comparison of the progeny will give clearer indications of local adaptation and its effects (see for example the work of Ennos et al., 1997) but these take time and space and are unfortunately rarely performed.

We have amazing abilities now to detect variation down to the sequence level, but it is in relating that information to the practical needs of those tasked with conserving that considerable problems arise. Variation in a particular marker system or its lack need not necessarily have profound implications. The bemused agency member who has provided their £XK and wanted to know the answer to "Life the universe and everything" will get a nice UPGMA analysis and be none the wiser, a problem which has to be addressed from both sides. Genetic studies are expensive and rarely give direct answers to practical conservation problems – they are however vital and useful if the right questions are asked!

As we have few truly endemic species then attention has been drawn to the preservation of local adaptations; genes, alleles or their complex expressions which may be specific to a site or region within the British Isles – the loss of which would deplete a species overall diversity. Our knowledge of the genetic variability of our flora is scant and with distinct taxonomic bias, it is therefore very difficult, if not impossible to predict a priori which species will be genetically interesting, or where the major part of that interest may lay.

Do all species show local adaptiveness and will that be threatened by introduced genotypes? This is difficult to answer, given the state of our knowledge on the genetics of the majority of the British flora, so a precautionary principle is best employed. However, we should not assume that individuals are necessarily best adapted to the environment in which they are growing. Colonisation is a chance event; gene pools will be restricted through founder effects and source populations may themselves already be genetically depauperate and maladapted.

Matings are usually non-random, with pollination restricted through lack of pollinators. Furthermore, once numbers reach low levels and populations become fragmented then stochastic factors can play a more dominant role. A plant's presence in an area therefore only tells us that it has been able to survive the conditions since its arrival/generation, not that it is well adapted. Introductions/alien genomes are not necessarily less well fitted to a novel environment, although it is likely that in some aspect they will be and this can lead to such difficulties as outbreeding depression.

We must also consider scale; local adaptation can be very local! Gene-flow, or indeed its absence, can create genetic structure at many levels and we must appreciate the likely scale before devising sampling strategies, or pro-active management. Populations may occupy square kilometres or square centimetres. These factors must also be considered in debates over "local provenance" where an easy to apply geographical criterion may be less appropriate than a more considered ecological approach. Proximity does not always equate with genetic similarity and species need to be considered on a case by case basis.

Are augmentations/ introductions good or bad in principle, and if bad is it still a necessary evil?

Any such manipulation will destroy the natural but yet largely understudied pattern of genetic variation in the British Isles. The potential damage is difficult to assess/quantify, whereas the short-term benefits may be more clearly seen. Intervention is only going to be appropriate/suitable in a proportion of cases and one has to use a common-sense approach based on the species biology and ecology. The ability to make this decision may however rely on the possession of far more knowledge than we currently possess. If our long-term aim is for survival and increase, then we may have to intervene even if this means a loss of "purity". Indeed that very purity may be at the root of the problem. Loss of habitat/ fragmentation and stochastic factors have reduced many of our species to reproductive incompetency, only their ability to persist (eg as long lived perennials or by vegetative propagation) masks the catastrophic nature of their situation. They now have little or no ability to disperse to new and often increasingly distant environments which may be ideal for them. A prime example is *Linnaea borealis* which has isolated self-incompatible clones, but this is far more widespread a problem amongst the bryophytes where the incidence of dioicy is great and many species are known only as single sexes. A less clear-cut case can be made for intervention where we have small, perhaps monoclonal populations of taxa which are preferentially outbreeding. There is perhaps a salutary lesson to be learnt from two contrasting programmes in the Chilterns. One programme sought to maximise heterozygosity as it had been shown that inbreeding had been the chief cause for failure to increase, stock was thus taken from several sources and the introduction flourished. The second scheme saw a detailed genetic study find differences between the two remaining critically small local populations, but not before material laboriously raised from site A had been equally laboriously introduced to site B where it's progress was being monitored. As a result of the discovery it was all removed for fear of corrupting the natural patterns of genetic variation. A sensible step or not? Given that the genetics of each individual was known, its location mapped, long-term monitoring could be maintained and the species is in all probability preferentially outbreeding, I doubt it. When I see military orchids prospering as well as red kites I'll be more inclined to agree with the purist view!

If properly resourced and sympathetically performed on the back of the appropriate research, necessarily with a genetic component, then I think augmentation, even introduction to novel sites both inevitable and advisable. However, several caveats need be added. We must understand the consequences of our actions better and have a better knowledge of that we seek to influence. There is no point embarking on an augmentation or introduction programme without understanding the causes of decline or extinction (although arguably these may only become clear following monitoring of experimentally manipulated populations). Intervention should also only be attempted where there is a reasonable expectation that the population(s) will become self-sustaining with minimal management.

Unfortunately there are few positive examples of the benefits of plant introduction programmes to present to the sceptical, and several rather embarrassing failures. I suspect this is because many have taken place in an ad hoc fashion, on too small a scale, with inadequate follow-up/ integration into site management and hide-bound by strictures. The starfruit (*Damasonium alisma*) recovery programme managed by Plantlife exemplifies one difficulty. Re-introduction, ie the return of a plant to an area from which it has become extinct attracts less brick-bats than introduction to novel areas. The difficulty often is that former sites are no longer suitable (if they were the species would possibly still be there!) whereas novel sites may be. The only population of *Damasonium* flowering in the last few years has been an introduction. By taking a pro-active approach to its conservation we are only emulating the dispersive role once performed by livestock in a less fragmented world.

The British landscape is artificial - we have always been the gardener, if unwittingly, it is now time to acknowledge that and manage our land and the species we choose to retain accordingly.

Why use spatially explicit and direct gene flow approaches in conservation genetics?

Andrew Lowe, Centre for Ecology and Hydrology

There is a close interdependency between genetic structure and gene flow in plants. Consideration of gene flow is important for the genetic resource management of plants because lack of gene flow between populations leads to isolation and drift, but increased gene flow can increase effective population size and help maintain genetic diversity. Several intrinsic and extrinsic factors influence gene flow and the consequent partitioning of genetic variation across the range of a species, including; mating system, seed and pollen dispersion strategies, population density, regeneration dynamics, other ecological factors, and size of and distance between populations.

Genetic structure has traditionally been calculated from co-dominant marker data using Wright's F statistics, which describe the proportion of variation partitioned within and between populations (F_{ST}, which varies between 0 and 1). For nuclear encoded data, gene flow parameters (Nm) can then calculated from genetic structure estimates using the formula $F_{ST} = 1/(4Nm + 1)$. In general the influence of 1 migrant per population (Fst approx. equal to 0.2) is enough to offset the effect of genetic drift and differentiation between populations. However, there are several problems with this method of estimating gene flow, including; assumes uniform ideal system, assumes equal population sizes and distances, doesn't allow for mutation (infinite allele model), produces summary statistics of gene flow calculated from genetic structure which is a consequence of a life time of population influences, produces population based not individual based estimates, estimate is static not dynamic.

Whilst the above are useful summary statistics for describing genetic connectivity between populations, recent advances in DNA methods (highly polymorphic markers allow individual based fingerprinting) and population analyses (autocorrelation analysis of genetic variation and exclusion and maximum likelihood methods of parentage assignment) have allowed further insights of genetic structure and gene flow within and between populations. Advantages of such systems are that they provide a much more accurate description of gene dynamics in an environment (ie not static). In addition, comparisons of indirect and direct estimates of gene flow are informative on several scales; individual (variation in reproductive success), annual (variation in gene flow), generation (selection pressures, inbreeding/outbreeding depression). However, such direct methods also have disadvantages, including; it is individual not population based approach (although data can be analysed in several ways, including the calculation of population estimates), mainly done on trees due to certainty of sampling, a lot of work to develop markers and screen large numbers of individuals required for good study, expensive and time consuming. Mainly due to the latter constraints of time and money, such studies are only reserved for the most important case studies and for reference setting.

Three case studies are presented to demonstrate the potential application of direct gene flow methods for prioritising conservation genetic strategies.

1. Pollen and seed-mediated gene flow are estimated directly within and outside a continuous forest canopy of European oaks, and used as inputs for simulation models to examine colonisation and regeneration dynamics under changing land-use systems.

2. Pollen-mediated gene flow is analysed for mahogany within a recently fragmented forest landscape in Costa Rica. Intuitive impacts of habitat fragmentation include loss of genetic diversity (rare alleles) from smaller forest blocks, but non-intuitive results include increase in gene flow between more isolated and smaller blocks of forest (probably connected with a change in pollinator across open grassland) which may promote maintenance of diversity between forest blocks once land-use change has halted.

3. The discrete and patchy distribution of blocks of ancient ash and rowan forest are being studied in the complex topography of the Carrifran Wildwood valley. Pollen and seed-mediated gene flow estimates will be interpreted in the context of wind direction and speeds for helping inform replanting activities to establish native forest corridor schemes.

Session Three: Conservation case studies

Genetic variation and conservation of *Woodsia ilvensis*

Stuart Lindsay, Adrian Dyer, Phil Lusby, Andy Ensoll, Mary Gibby, Royal Botanic Garden Edinburgh

Johannes Vogel, Fred Rumsey, Natural History Museum, London

Woodsia ilvensis is classified as ‘Endangered’ in Britain. It occurs in mountainous areas where there is a cool, continental climate, and is much more widely distributed in Scandinavia and the Alps. In Britain it grows in rock crevices or in freely draining pockets of soil among crumbling rocks or scree. There are fewer than 120 plants or ‘clumps’ known, and many populations are very small. Although plants can be long-lived there has been no evidence of recruitment into known populations in recent years. Added to this, some populations are in unstable sites, and could easily be lost through rock fall. Plants may also be vulnerable to grazing. The fern has never been common in Britain but, like other rarities, suffered from over-collecting during the Victorian fern craze. A research programme was established, with funding support from The Leverhulme Trust, to develop an appropriate conservation plan for the species in Britain, and it focussed on surveys of extant and historical sites, determination of spore viability and reproductive capacity, and exploration of population genetic structure. The survey revealed the presence of some 114 clumps, distributed in England, Scotland and Wales. Spore samples from several populations proved to be viable, and a large ex-situ collection of sporophytes was established at the Royal Botanic Garden Edinburgh. Low levels of allozyme variation were found in all populations of *W. ilvensis*, including those from Norway. The greatest diversity was found in Wales, despite a small population size (n=13). With the availability of the ex-situ collection of sporophytes, re-introduction was considered at sites where the species is extinct, or to augment existing populations. Over 200 plants have now been introduced to two historical sites in England, using a mixture of plants of British origin, and at a third site in Scotland using plants of local provenance to augment the very small population close-by. Monitoring over two years shows a survival rate of c. 90%.

The project illustrates the importance of sharing information from research on historical distribution, reproductive capability and population genetic structure with the conservation agencies to develop appropriate strategies for conservation, implementing re-introduction or augmentation where appropriate.

Euphrasia

Graham French, Royal Botanic Garden, Edinurgh

The genus *Euphrasia* represents a group of annual hemi-parasitic plants whose taxonomic treatment remains problematic, with difficulties defining appropriate species boundaries. In Britain, having the highest diversity of *Euphrasia* in Europe, this difficulty in species delimitation is especially relevant. A significant proportion of this diversity has originated in Britain, with the result that, out of the currently described 19 species, at least a third are endemic and considered to have high enough conservation importance to be included in the Biodiversity Action Plan short list for vascular plants. Within British *Euphrasia*, the inclusion of six endemic species, though accounting for almost a quarter of the vascular plant species on the high conservation status BAP short list, may still not be an adequate representation of its unique diversity as, by applying the current species concept, many more discrete taxonomic units could be equally recognised and included.

This genus therefore highlights an important issue when defining conservation priorities and ultimately the distribution of limited conservation funds. Should priority be given to reducing the extinction of unique evolutionary units, presently defined within species concepts or to the protection of underlying evolutionary processes and thereby help to safeguard the generation of future biodiversity?

In a rapidly evolving genus like *Euphrasia*, the latter conservation approach may be more appropriate. This approach increases the importance of a better understanding of evolutionary processes, such as mating system, hybridisation and gene flow across ploidy levels, when deciding conservation priorities. Molecular techniques, by offering unique insights into these evolutionary processes, may therefore be increasingly seen as an important initial tool in setting conservation priorities, both in the genus *Euphrasia* as well as plants groups in general.

By answering the following questions, molecular research, undertaken both at the Royal Botanic Garden Edinburgh and University of Edinburgh, aims to gain an insight into some of the processes that have helped generate the high diversity seen in British *Euphrasia*.
•Are there differences in breeding systems, producing a mixture of inbred lines and outbred taxa?

- •Do genetic discontinuities match phenotypic discontinuities?
- •Are there reproductive barriers related to ploidy level?

Work done to date, using plastid PCR-RFLPs, have defined 15 haplotypes across 66 populations taken from 17 out of the 19 species, across Britain. Unique haplotypes were present in the differing ploidy levels. This supports the strong reproductive barrier between diploid and tetraploid species found by cross-fertilisation experiments, performed by Peter Yeo in the 1960's. Otherwise no plastid partitioning were found in relation to defined species or geographical areas.

Microsatellite loci have also been developed to enable future study of the breeding system in relationship to variation in corolla size amongst diploid species. Future work will also include the use of AFLP genetic fingerprinting technique to examine the presence of genetic discontinuities, their relationship to phenotypic discontinuities and whether the diversity of morphotypes have originated locally or resulted from longer distance dispersal. The combination of these results will contribute to the improved targeting of future conservation resources in this genus, either guiding conservation priorities towards protection of endemic populations or to the safeguarding of processes that are generating local diversity, including the protection of local populations and habitats, with special importance for areas with high morphological diversity.

Military and monkey orchids – what do we have in England?

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Of the five species of *Orchis sensu stricto* found in Britain, only one (*O. mascula*, early purple orchid) is widespread and common. The remaining four species are southern English specialities. *Orchis anthropophora* (man orchid) is relatively frequent in Kent with scattered records elsewhere and *Orchis purpurea* (lady orchid) is a also a speciality of Kent, where it can be locally frequent. *Orchis simia* (monkey orchid) and *O. militaris* (military orchid) are now both extreme rarities in England, each known from only a small number of populations, *O. simia* in Kent and Oxfordshire and *O. militaris* in Buckinghamshire, Oxfordshire and Suffolk. *Orchis militaris* was thought to be extinct from the 1920s until its rediscovery first in Buckinghamshire in 1947 and then in Suffolk in 1955.
We have compared the English populations of *O. simia* and *O. militaris* to each other and to Continental material using DNA sequencing and two genetic fingerprinting methods: amplified fragment length polymorphism (AFLP™) and plastid microsatellites. AFLP is a multilocus fingerprint technique, providing information from the nuclear genome (inherited from maternal and paternal parents). In contrast, plastid microsatellites are single-locus markers, providing information from the plastid genome (found in chloroplasts and other plastids, and this is inherited from the maternal parent only in most flowering plants.

AFLP show English populations of *O. militaris* to be distinct from each other and from the Continental populations tested. The site in Oxfordshire had been thought to be derived from the nearby Buckinghamshire site, but our results show them to be clearly distinct. Also surprising was the discovery that the small Oxfordshire population showed almost as much genetic variation as the much larger Buckinghamshire population. In contrast, the large population in Suffolk shows very little genetic variation, probably the result of recent long-distance dispersal from a Continental population, followed by successful establishment from a small number (possibly as low as one) original plants.

Plastid microsatellites showed a somewhat different pattern, with the Buckinghamshire, Suffolk and Continental populations all showing the same cytotype, whereas the Oxfordshire population had a cytotype not recorded elsewhere from *O. militaris*, thus confirming its distinctness from the Buckinghamshire population.

DNA sequencing further complicates the story. For *O. militaris* and *O. simia*, sequences from the ITS region of nuclear DNA are of two different types, but the split is not between the species. All plants of *O. militaris* tested have the same type, and this matches the type found in 'northern' *O. simia* (English, Dutch and northern French plants). Southern French material of *O. simia* had a different type.

Our preliminary study of sequences from the *trnL-F* region of plastid DNA show the same split into two different types, with all *O. militaris* material studied so far having the same type as northern *O. simia*, and southern material of *O. simia* (from Crete) has the different type.

These results indicate that there has been some historical introgression between *O. militaris* and *O. simia*, caused by hybridisation between the two species, followed by crossing between members. The hybridisation may have taken place in refugia during the last glaciation.

In terms of conservation policy, it appears that populations of these two species are distinct in England (and the parts of the Continent close by) and that these are worthy of conservation. Particularly noteworthy are the distinctness and genetic variability of the Oxfordshire population of *O. militaris*. Further afield, more study is required of southern material for both species before the full extent of current and historical hybridisation can be ascertained.

We gratefully acknowledge Professor John Parker (Univ. of Cambridge), who contributed to the early part of this study.

Summary

Barbara Jones, Countryside Council for Wales

This workshop has demonstrated that important research is currently being undertaken in the sphere of conservation genetics, but that there is room for improvement in many aspects. A number of issues have been raised which require consideration by conservation bodies and researchers alike if we are to progress in making the field of conservation genetics more applicable and relevant to the general work of conservation in Britain. Many of these are self evident, but re-emphasising their role and importance is useful to enable this workshop to produce recommendations and move forward towards integrating genetics as a component of conservation related decisions, where appropriate.

These issues include the education of conservationists in the importance of genetics in their field of work and also the education of researchers in the needs of conservationists. One can often expect the other to understand their needs and requirements, but this is not easy because of the very different nature of these two areas of work

Discussions on the integration of genetics with more traditional ecological and biological survey/research are needed to ensure that a polarity between the two does not develop. Genetics is a part of the biological/ecological world which should be used when appropriate to ensure that conservation policies are developed according to sound genetic principles.

The development of a large (European) scale programme would be constructive, to consider wide ranging genetics research to cover issues such as the effects of climate change, the evolutionary history of threatened species and how British species sit in the context of a wider perspective. Linked in with this is the need for larger scale studies of the UK flora, particularly of common species. Genetic conservation research often focuses on rare species. These studies are important in themselves to ensure that the most appropriate management is undertaken in any rescue or reintroduction schemes, however, studies of common species are also needed, for example to assess the existence of unique alleles or the validity of the general concept of low variation being a problem.

Monitoring of the genetic results and effects of management interventions (restoration/importation of material) is important to assess the success or otherwise of the intervention and to provide data for future work. Any interventions must be backed up by sound ecological and genetic studies and the practical reasons for decline or disappearance of a population must be addressed. Similar reasoning can also be invoked for the use of genetics to help manage invasive species in a discipline that relies currently on what is effectively a ‘slash and burn’ culture.

A useful review would be to investigate the representation of genetic variation in priority species within protected areas. It is usually easier to control management, conduct research and conserve species in such areas, so we need to know the amount of genetic variation which would be conserved in this way. Would it protect most or a small proportion of variation present and what does this mean for conservation in the wider countryside?

Finally, it would be useful to publicise references/case studies where genetics has been useful in formulating conservation decisions, for example on BAP species, to indicate the possibilities of such work. The presentation of results from any such conservation genetics research on vascular plants should be presented in management related terms and reports should include a section on the consequences of any results for future management of the species, not only to answer the particular question being addressed but also to increase the overall relevance and understanding of this important tool in the conservationists' armoury.

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Top left: Using a home-made moth trap.
Peter Wakely/English Nature 17,396
Middle left: Co_2 experiment at Roudsea Wood and Mosses NNR, Lancashire.
Peter Wakely/English Nature 21,792
Bottom left: Radio tracking a hare on Pawlett Hams, Somerset.
Paul Glendell/English Nature 23,020
Main: Identifying moths caught in a moth trap at Ham Wall NNR, Somerset.
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