If the parasitism insurance hypothesis is valid, one wonders why selection has produced such an inefficient response to the occasional overcrowding caused by CBP. Power et al. suggest that two other responses would be superior. First, starlings might reject parasitic eggs. Although Power et al. are uncertain about the reasons for the lack of widespread egg rejection, Evans[9] believed that most starling eggs are too similar to one another for rejection to be viable. Secondly, starlings could be indeterminate layers and lay just enough eggs so that the final clutch of host plus parasitic eggs is optimal, i.e. six. This would produce an optimal clutch when CBP does not occur. But starlings are determinate layers[6] and do not adjust their laying to the number of eggs in the nest.

Other adaptations that would seem superior to always laying a suboptimal clutch size are for a parasitized host to lay its extra egg(s) parasitically[10], or to eject enough eggs from overcrowded clutches to reduce them to the optimal size[11], or to increase the time span over which eggs hatch by beginning to incubate before egg laying is over. The latter would decrease the competitiveness of the last nestling to hatch, and thereby kill it off quickly in an overcrowded nest before it seriously depleted the food for other nestlings. Because starlings begin incubating with the penultimate egg[12], an even earlier onset of incubation should be possible. These last two strategies would usually waste a host egg when CBP occurs. However, eggs are relatively cheap for birds to form[13], and the more frequent benefits gained when CBP doesn't occur would undoubtedly outweigh the costs.

Could the parasitism insurance strategy be applicable to other species? Much of what we know about clutch-size determination is based on birds that are colonial and/or that nest in boxes, because such species allow researchers to study large samples of nests. These situations are precisely the ones in which CBP seems most prevalent in altricial species[3,4,6,9–11,14–17]. Although there is little or no evidence for CBP in some groups such as tits (Parus spp.)[4], which nest in boxes and have been classic research subjects for avian biologists, the critical molecular studies that provide the most feasible definitive test for CBP have not been done. So, researchers studying other species should at least consider the parasitism insurance hypothesis.

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Population Management for Conservation

Georgina M. Mace and Jonathan D. Ballou

As habitats disappear, the natural ranges of many animal populations become limited and fragmented to such an extent that extinction factors associated with small population size become significant. Interactions between various intrinsic and extrinsic extinction factors can lead to further risks in 'extinction vortices'[1]. In the future, we can expect more and more species with restricted habitat ranges to require an increasing amount of intensive management to ensure survival. The development of techniques for assessing threats, analysing populations for their susceptibility to these threats and designing appro-

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priate management techniques is therefore now an important area in conservation biology[2].

At a workshop meeting hosted by the National Zoological Park in Front Royal, Virginia, USA, late last year, population managers, theoretical population biologists, demographers and geneticists met to discuss methods for managing small populations for viability. The workshop, entitled 'Analytical Methods for Population Viability Analysis and Management', aimed to re-assess some of the goals of long-term population management[3], and especially to review techniques appropriate under various kinds of uncertainties that dominate much of conservation planning. The meeting was organized around four topics: pedigree analysis, demographic analysis, molecular genetics, and goals and management strategies.

Over both the short and the long term, population viability undoubtedly depends upon managing and retaining genetic variation, but within such generally defined goals there are numerous complexities, which were considered by the pedigree analysis panel. Jon Ballou described some statistical measures based on mean kinship, which are used for identifying genetically important individuals in the management of the captive and reintroduced golden lion tamarins (Leontopithecus rosalia)[4], and Robert Lacy (Chicago Zoological Society) outlined some simple statistics that summarize extended pedigrees and aid in assessing alternative management strategies. All genetic models make simple assumptions, and Elizabeth Thompson (University of Washington, Seattle) addressed one common assumption made in pedigree simulations, where the probability of retaining a particular gene is directly equated with the overall proportion of the genome retained. Alun Thomas (University of Bath) presented a method from image processing that can be applied to estimating unknown genotypes in extended pedigrees.

On a more practical level, colonial and group-living species pose problems for management in that individuals can rarely be monitored or managed. Also, there may be conflicts between retaining genetic diversity and maintaining natural patterns of social behaviour. Frank Princée (National Foundation for Zoological Research, Amsterdam) described some management techniques for social species based around maximum avoidance of inbreeding, and discussed how further extensions of this work can incorporate different genetic goals.

The demography panel considered many different aspects of population dynamics and subdivision. Mike Gilpin (University of California, San Diego) explained how demographic factors often pose more immediate threats than the genetic ones that have received most attention in recent years. Torbjörn Ebenhard (University of Stockholm) outlined the importance of demographic stochasticity, and introduced a concept of 'demographic effective population size' to incorporate its effects into population models. For most small population studies, simulation methods are most appropriate, not only for estimating population growth and extinction rates, but also for monitoring and maintaining stable populations. However, estimates of demographic parameters for these models are seldom available for poorly studied rare species.

Methods based on simple model curves have been applied in human and primate demography and were described by Bennett Dyke (Southwest Foundation, Texas) and Tim Gage (SUNY, Albany, New York). A similar approach has been adopted in marine mammal studies; Jay Barlow (National Marine Fisheries Service, La Jolla, California) showed some methods of curve fitting that could be applied to many wild and captive populations. Barbara Taylor (University of California, San Diego) applied these techniques to some populations with poor and missing data such as the captive Przewalski horse (*Equus przewalskii*) herd. An alternative and pragmatic approach is to identify more easily measured life history characteristics that are good estimators of more formal demographic parameters, as described by Andy Dobson (University of Rochester, New York) for some studies on wild vertebrate populations.

Molecular genetics seems at first sight to offer enormous potential for conservation biology, but several speakers urged caution. As Oliver Ryder (San Diego Zoological Society)

and John Avise (University of Georgia) both illustrated, there is a variety of techniques available, and all cannot be applied to the divergent problems in conservation. Some long-established genetic techniques of relatively low cost and difficulty, such as allozyme studies and karyotyping, still have great utility, especially for studies of population substructure and phylogeny. However, there is enormous potential for nuclear and mitochondrial DNA studies to contribute much more[5], as Steve O'Brien (National Cancer Institute, Maryland) showed in his studies on the genetic structure of wild cat species.

The role of hypervariable DNA probes is still unclear. While they have an undoubted use in individual and family studies, both Mike Lynch (University of Oregon) and Charles Geyer (University of Seattle) described the difficulties in making population genetic assessments from multi-locus hypervariable probes[6].

Unfortunately, perhaps the most difficult level of genetic analysis concerns overall relatedness. That this is also an area of major interest was demonstrated by Susan Haig (University of South Carolina) in her presentation on methods for identifying unrelated and genetically diverse Guam rail (*Rallus owstoni*) individuals for reintroduction. At present, only pedigree analysis has been used[7], but molecular studies could contribute much more. One promising development discussed by Oliver Ryder is the polymerase chain reaction (PCR)[8] which will, under certain circumstances, enable large amounts of DNA to be amplified up from tiny amounts of tissue such as a single hair or sperm.

The final panel considered goals and management strategies for population management. Ulysses Seal (IUCN Captive Breeding Specialist Group, Minnesota) outlined a series of case studies — California condor (*Gymnogyps californianus*), black-footed ferret (*Mustela nigripes*), Rothschild's mynah (*Leucopsar rothschildi*) and Javan rhino (*Rhinoceros unicornis*) — that illustrate our past failure to manage threatened species effectively before they reach critically low numbers. Management is needed while numbers are still in the thousands, and this will involve altering our views of conservation action in a variety of ways. First, recognition of endangered status needs to be refined along sound biological principles; Georgina Mace presented some ideas on ways to categorize species when few data are available.

Second, conservation action needs to be effectively enshrined in legislation; however, as Kathy Ralls (National Zoological Park) showed, even in the USA, where there is quite elaborate legislation, there are problems and pitfalls in interpreting the letter of the law.

A variety of genetic and demographic problems associated with intensive population management were discussed. Russ Lande (University of Chicago) described problems inherent in some of the current simple genetic goals based largely on heterozygosity for neutral loci, and these were further elaborated by Phil Hedrick (Pennsylvania State University). Lande described new methods for incorporating other kinds of genetic variation that may be significant for long-term population viability (e.g. additive genetic variation for quantitative characters and mutation), but stressed that in the short term the random factors affecting population size and structure are more significant[9]. He presented some simple models that may be useful in this context.

Steve Arnold (University of Chicago) discussed some of the biological difficulties in highly intensive population management, particularly through elimination of certain kinds of natural and sexual selection. This is likely to become significant for many more species when, as is increasingly the case, captive and wild populations are managed interactively for species conservation. Tom Foose (American Association of Zoological Parks and Aquariums) described programmes for the red wolf (*Canis rufus*) and black-footed ferret in North America, which are now based around both zoo and reintroduced populations. Adding another cautionary note, Nils Ryman (University of Stockholm) talked about problems in Atlantic salmon (*Salmo salar*) that have resulted from accidental introgression from captive to wild populations.

Two themes ran through the meeting. One concerned the use of population simulation models, which in many cases seem to offer solutions to the problem of how to predict and manage in the face of multiple uncertainties. The consensus was that population viability analysis is not a defined set of analyses, but rather describes a procedure for identifying weaknesses and threats. The types of analysis used and their accuracy and reliability will vary from case to case. Robert Lacy described one stochastic model, which he has applied to cases such as the Florida panther (*Felis concolor coryi*), that has proved

helpful in identifying critical factors for population management. Tony Starfield (University of Minneapolis) described another population simulation model and showed how a different approach to modelling is required when many parameters and their ranges are unknown. Unlike engineering applications, models should not be used to seek optimal solutions, but instead to identify and minimize risks. A policy of 'minimum regret' may be a good one for conservation biology.

A second theme was 'altered states', a term introduced by William Conway (New York Zoological Society) in his opening remarks. The world is changing rapidly, especially for wild species in tropical areas, and the conservation community will soon face a variety of new problems arising from the need to manage many species, even those in reserves

and protected areas. Long-term survival of many species will depend upon the development of principles very different from those presently adopted in wildlife management – principles that may conflict with our more traditional concepts of wildness and freedom. As intensive population management techniques start to incorporate both captive and reintroduced populations, the distinction between captive population management and management in reserves and protected areas breaks down. There are aesthetic and moral issues to be resolved in this area that are even more demanding than the biological ones.

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DNA and Morphology: Inference of Plant Phylogeny

Kenneth J. Sytsma

In recent years, there has been an increasing number of reports of discrepancies between analyses of DNA and morphology in the estimation of phylogeny. In plants, the discrepancies can be attributed to procedural problems (apparent discrepancies) or to biological attributes of the organisms (real discrepancies). The problems can arise from within both morphological and molecular aspects of the study. A better understanding of both kinds of problem permits a more thorough synthesis of DNA and morphology in the inference of plant phylogeny, and can result in the further refinement or resolution of a morphologically based phylogeny by molecular evidence, and of a molecularly based phylogeny by morphological evidence.

In the past decade, DNA-based inference of plant phylogeny has developed into a multi-faceted systematic endeavor. Although this approach is recent, it has already had a significant impact on many levels of plant systematics[1-3]. The great interest in, and major movement toward,

the use of DNA in phylogenetic studies of plants raises the question, 'Why is molecular evidence so appealing in plants?' The appeal comes from several beliefs, justified or not, concerning DNA and morphology: (1) that molecular analysis provides numerous and independent characters whereas morphological analysis provides fewer characters, often of questionable homology; (2) that morphology, unlike most DNA regions, is prone to considerable convergence; (3) that the genetic basis of convergence in molecules is better known; and (4) that molecular analysis is free of the subjective kinds of character analysis and outgroup selection that might mislead morphological analysis. As Patterson[4] aptly queried, 'have molecules superseded morphology as guides to the history of life, or are the approaches sides of the same coin, with same problems and limitations? Do molecules and morphology give the same picture of the history of life, or two more or less distorted views of the same

recently examined for animals[4,5], but the situation in plants is unresolved.

The primary goal in phylogenetic studies is to infer the single historical genealogy – i.e. the true phylogeny – of a group of organisms. It might thus be expected (1) that systematic studies of any set of genetically determined characters within a group of organisms should be congruent with other such studies based on different suites of characters, (2) that congruency provides strong evidence that the true phylogeny has been inferred, and (3) that conflict among the results may indicate low resolution power of the data sets, invalid and inappropriate

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Box 1. Causes of apparent or real disparity between DNA and traditional methods of inferring plant phylogeny

Procedural problems
(1) Equating overall similarity with phylogenetic relationships
(2) Equating crossing relationships with phylogenetic relationships
(3) Inappropriate molecule(s) for taxonomic level or question

Biological problems
(4) Unequal rates of morphological evolution
(5) Convergence of morphological characters
(6) Hybridization and/or introgression
(7) Polyploidy