a breeding population at one site; zoos compete over animals for display purposes; maintaining animals in zoos is expensive; there is still no reasonable time frame for return of captive-bred animals to the wild. Since 1985 captive breeding schemes for Sumatran rhinos have resulted in the capture of 27 animals in Indonesia and Malaysia. Nine of these animals (33%) have died and there have still been no successful births as a result of the breeding scheme though it is hoped that the Ragunan female (Jakarta) is now pregnant. The zoo option is the most expensive in terms of funding and resources yet is probably the least likely to succeed. Nor does the zoo option remove the necessity or responsibility of strengthening management of the conservation areas. When the present contract between PHPA and SRT expires, the programme should be independently evaluated for its contribution to rhino conservation efforts.

5. Conservation Activities

For Sumatran rhinos conservation activities in order of priority are:
1. better protection and management of conservation areas
2. better protection of rhinos inside and outside reserves (strong anti-poaching measures)
3. translocation of 'doomed' rhinos to reserves within their previous range and better management of those reserves
4. breeding of translocated Sumatran rhinos under semi-wild conditions
5. captive breeding schemes in zoos

Javan Rhino

The Javan rhino once occurred throughout Asia from Assam to Indochina and Java. Today Javan rhinos are known to occur only in two localities, Ujung Kulon N.P. (60 animals) in West Java and in South Vietnam in Nam Cat Tien N.P. (5-15 animals). The Javan population is possibly the only viable population in the world. That rhinos still occur on the densely-populated island of Java is a tribute to the commitment and far-sightedness of the government of Indonesia which has allocated considerable resources longterm to Ujung Kulon N.P. There are no Javan rhinos outside the conservation area.

Conservation options for the Javan rhino are four: in-situ conservation in Ujung Kulon N.P., translocation of rhinos within the park e.g. to Gn. Honje or to other parks within the rhino's previous known range, captive breeding in semi-wild conditions and captive breeding in zoos.

1. In-situ conservation

a. The first priority for the Javan rhino is in situ conservation in the park by improving protection and management. Already this prescription has shown some success. In 1967 the Javan rhino population was estimated to number only 25 animals; with improved protection and managment the population has doubled. Better protection of Ujung Kulon protects not only the rhino but also one of the last remaining blocks of lowland rainforest on Java, three endemic species of primates, many rare plants, half the Javan bird list and threatened reptiles such as crocodiles and marine turtles.

b. The eastern part of Ujung Kulon N.P., the Gunung Honje area is little used by rhinos at present. This is probably due to extensive human disturbance in the area. Better protection of the eastern part of the park to reduce disturbance will increase the rhinos' potential range. Rhinos could be allowed to repopulate this area naturally or rhinos could be translocated to Gn.Honje.

2. Translocation

There has been considerable speculation that the Javan rhino in Ujung Kulon may be at carrying capacity. Prior to any removal of animals, there must be a thorough longterm research programme to determine the status of the rhino population and its limiting factors. If the rhino population in Ujung Kulon is determined to have reached carrying capacity then some animals can be captured and translocated to other areas or reserves within the rhino's former range e.g. Gn. Honje or Way Kambas N.P., Sumatra. Since all capture programmes involve high risks, only very small numbers of animals (4-6) should be removed initially from the Ujung Kulon population.

3. Captive Breeding under semi-wild conditions

As part of the translocation programme captured rhinos could be used to found a semi-wild breeding population. As with the Sumatran rhino, the best option would be to establish a breeding programme under semi-wild conditions in a very large enclosure of suitable habitat within the rhinos' former range, e.g. Gn. Honje or Way Kambas. Such a programme should only be undertaken after extensive research to determine suitability of the receiving habitat and availability of known rhino food plants. Pulau Panaitan is probably not a suitable receiving site because of lack of surface water in many areas at the end of the dry season. Moreover rhinos were never recorded on Panaitan in the past.

4. Captive breeding in Zoos

a. The last option, as currently advocated by the CBSG, is a zoo captive breeding scheme, involving the capture of 18-26 rhinos. **It is the considered opinion of the senior scientific advisors of the WWF Indonesia and WWF Asia Programmes, as well as many other concerned and eminent scientists, that the zoo option is by far the worst option from a conservation point of view. Such a scheme could itself threaten the survival of the Javan rhino in Indonesia.**

b. There are no convincing arguments for pursuing a zoo captive breeding scheme at this time. Re-analysis of the CBSG's own PVA data shows that the rhino population is more than 30 times more likely to go extinct if animals are removed to zoos than if a policy of in situ conservation is pursued. The zoo programme should only be reconsidered if poaching becomes a serious threat in Ujung Kulon and the population shows dramatic decline.

5. Conservation Activities

Conservation activities for Javan rhino in order of priority:
1. better protection and management of Ujung Kulon N.P.
2. better protection and management of the Gn. Honje extension to minimise human disturbance and encroachment.
3. Comprehensive longterm research to obtain accurate data on population numbers and status of Javan rhinos, whether the population is at carrying capacity and if so why (competition, availability of food plants). Research must be management-orientated.
4. Translocation of 4-6 founder animals to other reserves within the Javan rhino's former range. This involves strengthening protection and management of those reserves.
5. Captive breeding of Javan rhinos in semi-wild conditions within a conservation area. Options 4 and 5 can be complementary.
6. Captive breeding in zoos. This should not be undertaken at the present time but may remain as a future option. Any zoo captive breeding schemes should be carefully evaluated, focus on Indonesian zoos and be dependent on zoo facilities and success with breeding Sumatran rhinos.

WWF Commitment

The WWF Indonesia Programme is committed to assist PHPA with appropriate in situ conservation activities to protect Sumatran and Javan rhinos and the reserves where they occur.

Dr K. MacKinnon
Conservation Advisor

Dr C. Santiapillai
Senior Scientific Officer

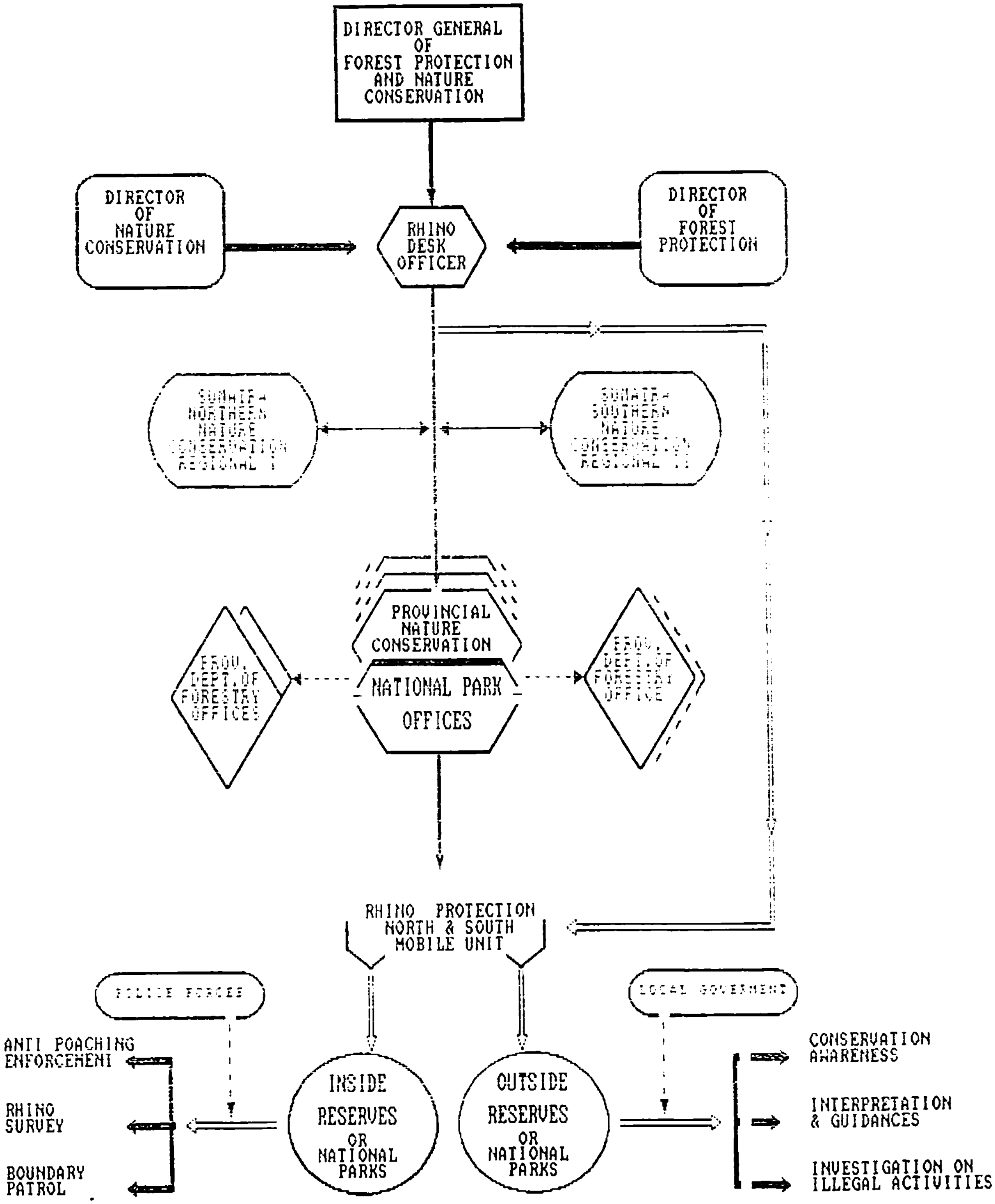
Dr R. Betts
Representative

January 1991

INDONESIAN RHINO PROTECTION MOBILE UNIT

ORGANIZATION CHART

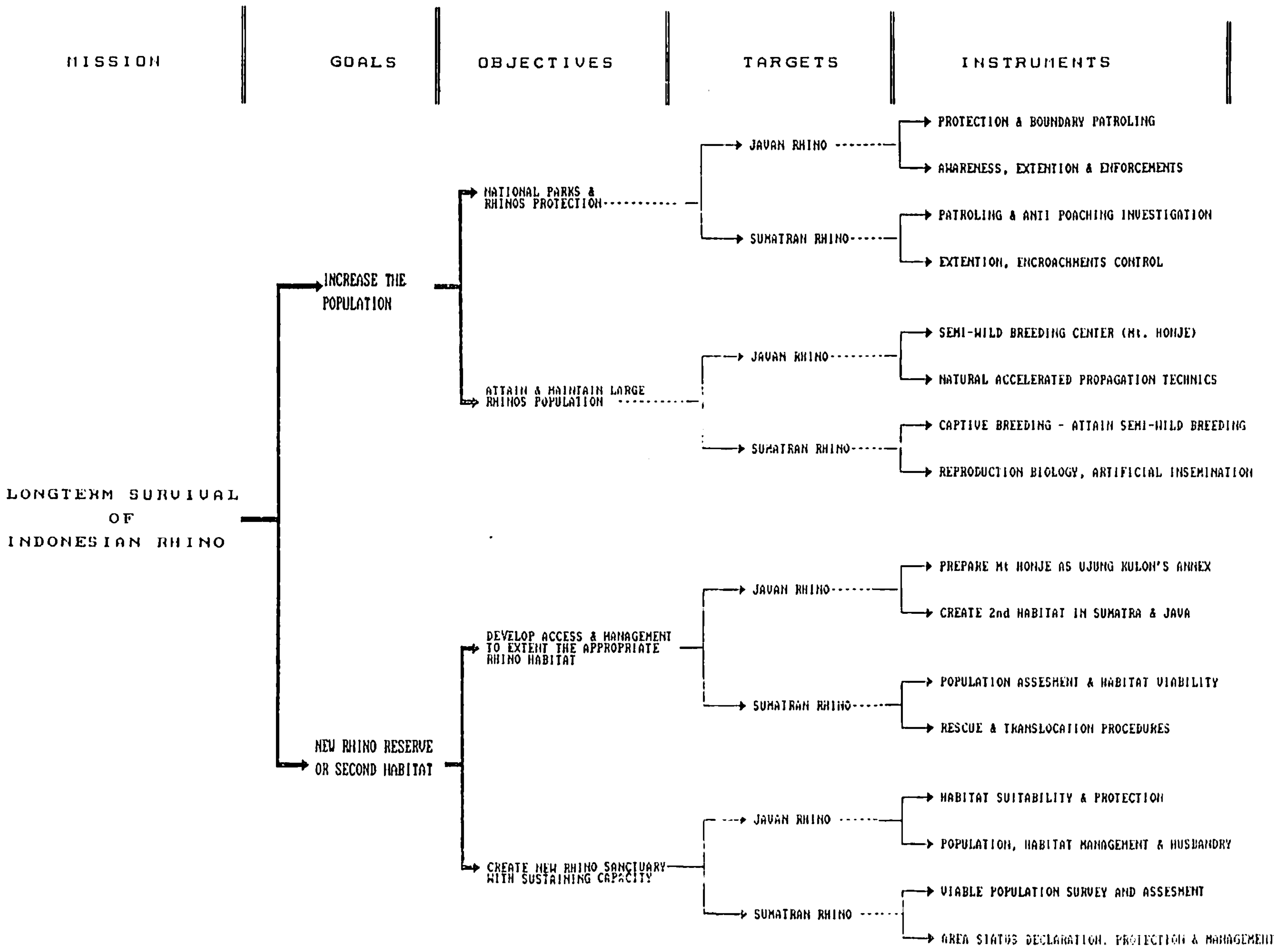
(4th EDITION)



INDONESIAN RHINO CONSERVATION STRATEGY

RELATIONSHIP ANALYSIS

(2nd DRAFT)



MISSION

GOALS

OBJECTIVES

TARGETS

INSTRUMENTS

LONGTERM SURVIVAL OF INDONESIAN RHINO

INCREASE THE POPULATION

NATIONAL PARKS & RHINOS PROTECTION

JAVAN RHINO

PROTECTION & BOUNDARY PATROLING

AWARENESS, EXTENTION & ENFORCEMENTS

SUMATRAN RHINO

PATROLING & ANTI POACHING INVESTIGATION

EXTENTION, ENCROACHMENTS CONTROL

ATTAIN & MAINTAIN LARGE RHINOS POPULATION

JAVAN RHINO

SEMI-WILD BREEDING CENTER (Mt. HONJE)

NATURAL ACCELERATED PROPAGATION TECHNICS

SUMATRAN RHINO

CAPTIVE BREEDING - ATTAIN SEMI-WILD BREEDING

REPRODUCTION BIOLOGY, ARTIFICIAL INSEMINATION

NEW RHINO RESERVE OR SECOND HABITAT

DEVELOP ACCESS & MANAGEMENT TO EXTENT THE APPROPRIATE RHINO HABITAT

JAVAN RHINO

PREPARE Mt HONJE AS UJUNG KULON'S ANNEX

CREATE 2nd HABITAT IN SUMATRA & JAVA

SUMATRAN RHINO

POPULATION ASSESMENT & HABITAT VIABILITY

RESCUE & TRANSLOCATION PROCEDURES

CREATE NEW RHINO SANCTUARY WITH SUSTAINING CAPACITY

JAVAN RHINO

HABITAT SUITABILITY & PROTECTION

POPULATION, HABITAT MANAGEMENT & HUSBANDRY

SUMATRAN RHINO

VIABLE POPULATION SURVEY AND ASSESMENT

AREA STATUS DECLARATION, PROTECTION & MANAGEMENT

A STRATEGY TO CONSERVE INDONESIAN RHINOS

Kenneth R. Ashby (Durham)
Charles Santiapillai (WWF)

San Diego, USA
May 1991

A STRATEGY TO CONSERVE INDONESIAN RHINOS

Kenneth R. Ashby
University of Durham, UK

Charles Santiapillai
WWF. PO Box 133 Bogor, Indonesia

Javan rhino (Rhinoceros sondaicus) and Sumatran rhino (Dicerorhinus sumatrensis) differ in their conservation status. The Javan rhino is found in Indonesia only at Ujung Kulon National Park, but its numbers have doubled with improved protection since 1967 (Amman 1985) and a surviving group has been discovered in Vietnam (Dang 1986, Schaller et al. 1990, Santiapillai et al. 1991), whereas the Sumatran rhino, while still widely distributed is poorly protected and suffering rapid loss of habitat (Santiapillai and MacKinnon; Widodo et al. this conference).

A conservation strategy must aim for and balance:-

1. Effective protection of populations and habitats.

2. Minimising mortality and loss of breeding potential caused by trauma on capture or by bad management, disease and inbreeding depression.

3. Avoiding eduction in breeding success through crowding in restricted natural habitats.

Javan rhino - Aims:

(1) Given numbers in Ujung Kulon National Park at approaching the maximum rate observed elsewhere over a substantial period (for example, 8% per year in Chitwan National Park in Nepal, Kaziranga National Park in Assam, India and in Umfolozi National Park in South Africa), protection there should be further improved and nothing done to hinder recovery. The rhino density at 0.2 per km2 is likely to be well below the carrying capacity (rhino densities elsewhere include 3 per km2 at Kaziranga (Choudhury 1987) and 5 per km2 in parts of Chitwan (Laurie 1982). The proposal of the IUCN Captive Breeding Specialist Group (CBSG) to remove half the population from Ujung Kulon at present stage of recovery is a recipe for disaster. It would intensify all the threats to the population there of a stochastic nature, and cause gross disturbance.

The effects of inbreeding depression are real and thus of relevance to the situation at Ujung Kulon, but they are transitory, and are minimised if numbers recover quickly from bottlenecks (Templeton and Reed 1984). The population of 40± wild cattle at Chillingham in northern England is fit and thriving after 800 years (about 120 generations) of continuous inbreeding, which has included bottlenecks of one female and one male in 1760 following an epidemic, and eight females and five males in 1947 following an arctic winter (Whitehead 1953). Equally striking is the case of the collared lizards of the Ozarks (Templeton 1986) where colonies of 40± have experienced 4,000 years (about 2,000 generations) of inbreeding.

Removal of small numbers of rhino from Ujung Kulon for breeding elsewhere should be considered only after a further substantial increase in numbers has been achieved in situ.

(2) Concern is often expressed that Krakatau may erupt (as in 1883) with disastrous consequences for Ujung Kulon. This is given as a justification for removing Javan rhinos from Ujung Kulon. The threat from Krakatau is about equivalent to that to Naples from Vesuvius. Being a remote peninsula with a narrow link to the mainland, Ujung Kulon is more easily protected than are most national parks and reserves.

Sumatran rhino - Aims:

(1) The forests of the mountains of Sumatra protect alike rhino, other vital fauna, timber supplies for the coming centuries, and watersheds thereby ensuring adequate water supplies for a burgeoning human population. Their protection is first priority.

(2) A dispassionate assessment is needed of what can be saved of the lowland forest in Sumatra and Borneo, and of the proportion of the rhinos that can be protected effectively within it.

(3) Rhinos elsewhere should be removed as quickly as possible to effectively protected but underpopulated reserves elsewhere; or for captive breeding in zoos that offer the exacting and very long-term facilities required. Parameters with respect to captive breeding of rhinos include:-

(a) The larger the animal and the longer the generation time, the greater the difficulty and expense of captive breeding. Rhinos score badly on both counts, for example in comparison with Arabian oryx, where captive breeding was a critical success but nevertheless far from easily achieved, particularly when the time came to reintroduce the species to the wild.

(b) The record concerning the survival and breeding success of captive Sumatran rhino is deplorable and must be improved.

(c) Large zoos with ample financial resources may themselves be subject to a decline in fortune.

In Britain, the popularity of wildlife TV films and the spread of 'animal rights' sentiments threaten the survival of zoos, with the national flagship, the London Zoo currently facing closure due to loss of popular appeal.

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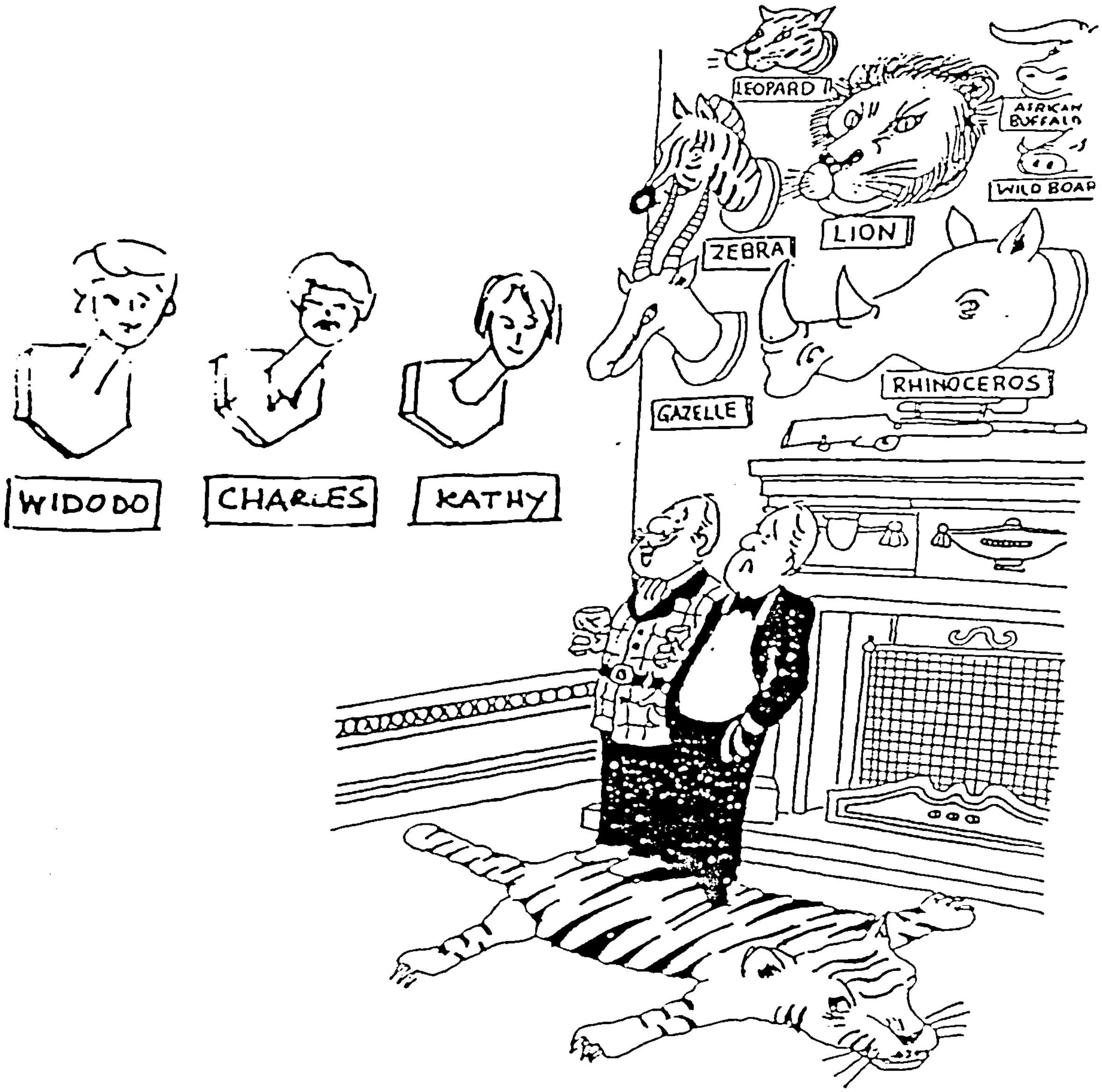

"I THOUGHT I'D BAG THEM BEFORE THEY BECAME EXTINCT"

INDONESIAN RHINO CONSERVATION WORKSHOP

BRIEFING BOOK

SECTION 9 - SAN DIEGO RHINO CONFERENCE

75th Anniversary of the Zoological Society of San Diego

INTERNATIONAL ▲R▲H▲I▲N▲O▲ CONFERENCE

SAN DIEGO 1991

RHINOCEROS BIOLOGY AND CONSERVATION

MAY 9 - 11, 1991

Hanalei Hotel
San Diego, California, USA

Oliver A. Ryder, Ph.D., Organizer
Center for Reproduction of Endangered Species
Zoological Society of San Diego
P. O. Box 551, San Diego, CA 92112 USA

INTERNATIONAL
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CONFERENCE REPORT

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INTERNATIONAL
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CONFERENCE
SAN DIEGO 1991

75th Anniversary of the Zoological Society of San Diego

RHINOCEROS BIOLOGY AND CONSERVATION

MAY 9 - 11, 1991
San Diego, California, USA

HIGHLIGHTS AND SUMMARY

The International Conference on Rhinoceros Biology and Conservation was the first conference to consider the plight of all five species of rhinoceros. Sponsored by the *Zoological* Society of San Diego, it was held May 9-11, 1991 at the Hanalei Hotel in Mission Valley. Over 30 countries were represented and the over 300 registrants included governmental representatives, zoo biologists, field biologists, representatives of non-governmental conservation organizations, veterinarians and academic scientists.

The conference attracted considerable media interest. Coverage included the New York Times, Los Angeles Times, San Diego Union and Tribune, San Diego television, CNN as well as by Science, Discover and New Scientist magazines. Radio interviews included local and state-wide Public Radio shows. KIRO radio in Seattle and Radio 2 in Sydney, Australia also conducted live interviews.

The basic scientific sessions included discussions of genetics, reproductive biology, veterinary medicine, and poster presentations provided new information about nutrition, disease, and other aspects of rhinoceros biology, including the first report of vocal communication in both African and Asian rhinos involving subsonic sounds.

Other technical sessions focused on the status of each of the five rhinoceros species, the development and implementation of plans for conservation of rhinos in separate nations in which rhino populations survive and the status of the four species of rhinoceros currently held in zoological parks.

Keynote addresses included the latest information on the international commerce in illegal rhinoceros products (Esmond Bradley Martin), the spiritual value of habitats with rhinos in an increasingly urban world (Rolf Benirschke), a strategic overview of what humans must really do to save the rhinoceros species (Mark Stanley Price), and a direct and personal plea from the Rhino Man, native Kenyan Michael Werikhe, for international assistance in securing rhino populations for the future.

Nearly 30 manuscripts were collected at the conference for the edited volume that will include the papers presented at the conference as well as additional contributions that were not included in the conference. This extensive book will be the first compilation of information on the biology and conservation of all five species of rhinoceros.

The conference office was busy on a nearly 24-hour basis. A conference news bulletin provided the latest information about the scheduling of working groups, revisions in the conference program, and other conference news. Summaries of the plenary sessions were entered into word processing files as were reports of working groups and draft resolutions. All these materials were combined and duplicated so that copies were available to all for discussion in the final plenary session. The reviewed and approved reports form the basis of the Conference Report that highlights the current situation for each species of rhinoceros and delineates directions for research, zoo and field conservation action. Thus, matters of consensus for conservation action as well as controversy in conservation methodology are made explicit and available.

CONFERENCE RESOLUTION

The Conference encourages the international donor community to consider the five species of rhino in Africa and Asia as flagship and umbrella species for conserving biodiversity and critical ecosystems. The critically endangered status of these species emphasizes the urgent need for immediate conservation action and funding. The Conference urges the donor community to use the Global Environmental Facility of The World Bank to fund conservation projects in Africa and Asia that protect rhinos and their habitats, involve local community participation in rhino management and conservation education and awareness programs.

(This resolution was unanimously approved at the final plenary session)

Keynote Addresses

Esmond Bradley Martin:	*The present-day trade routes and markets for rhinoceros products*
Rolf Benirschke:	*The spiritual value of habitats with rhinos in an increasingly urban world*
Mark R. Stanley Price:	*What will it take to save the rhino?*
Michael Werickhe:	*The rhino will live or die because of us*

Plenary I - Summary
Rhinoceros Evolution and Systematics: Conservation Implications

R. Aman, chair: *Genetic analysis of rhino populations in Kenya*
G. Amato: *Molecular evolution in rhinos*
M. George: *Mitochondrial DNA analysis of rhinoceros subspecies*
E. Harley: *Molecular Genetic studies of Southern African black rhinoceros*
D. Prothero: *Fifty million years of rhinoceros evolution*
O. Ryder: *Rhinoceros chromosomal studies: Application to gene pool conservation*
N. van der Merwe & A. Hall-Martin: *The determination of species and geographic origin of rhinoceros horn by isotopic analysis*

Fossil records indicate that the evolutionary history of rhinoceroses dates back to 50 million years ago. The newer molecular genetic techniques are quite useful in tracing the relatively recent evolutionary history of the five extant species of rhinos. What implications do those new techniques have from the conservation point of view? Here the concerns require a practical application of information gathered from such techniques. The questions may be: Is there a genetic basis for the species divisions at the sub-species level? Are such genetic differences between the sub-species large enough to contraindicate managing them at the sub-species level or are they small enough so that strategy of management could be dictated by factors other than genetic? Can these techniques determine with certainty the identity and relationships of individuals within a population? And from the point of view of regulation in trade of rhino products and forensics, can these techniques lead to identification of such products and trace their points of origin? It is clear from the proceedings that these new approaches hold great promise in providing answers to such questions.

Summary Report

This session opened with a brief description by Dr. Aman of efforts underway in Kenya in setting up a molecular genetics lab to conduct research on assessing genetic variation within large wildlife mammals within the region using a DNA-based approach. A project, in collaboration with Dr. Ryder and CRES, to examine genetic variation in black rhinos in Kenya has already been initiated. An interesting introduction on the subject of rhinos was provided by Dr. Prothero who traced back the evolutionary history of this family over the last 50 million years since its origin. Rhinoceroses were at one time dominant large land mammals on all the northern continents and in Africa and comprised over 65 genera that occupied diverse ecological niches. Today only five species in four genera survive.

Dr. Ryder described his work on analysis of chromosomes of the African rhino. Karyotypes of the northern and southern black rhino were found to be similar in terms of chromosome numbers but dissimilar when the proportion of biarmed chromosomes was examined. In a chromosomal survey of 7 black rhinos from Zimbabwe and 22 black rhinos from Kenya, the distribution of chromosome arm lengths was found to follow a bimodal pattern grouped according to origin. This may be reflecting changes in heterochromatin as a result of a recent lack of gene flow between populations in the two regions.

At the DNA level, low levels of intraspecifc variation are observed in the two African species of rhino. By analysis of mitochondrial DNA restriction fragment length polymorphisms, Dr. George found that the level of genetic variation ranged between 0 and 0.07% among northern white rhinos and between 0 and 0.04% among southern white rhinos. The differences between northern and southern white rhinos ranged between 1 and 1.4%. Much larger levels of variations ranging from 4.2 to 5% were observed between the white and the black rhino species. Using the same technique, Dr. Harley reported a similar level of sequence divergence of 6.8 ± 1.6% between the two species of African rhino which translated to a divergence time of 3.4 ± 0.8 million years. Harley also found that mitochondrial haplotypes that were unique to *D.b. minor*, *D.b. bicornis*, and *D.b. michaeli* could be defined and could serve as useful markers for those subspecies. He noted that the amount of divergence between the black rhino sub-species represented by these changes was small. Thus, there was no indication to maintain these subspecies separately based on mitochondrial DNA distance estimates. Any outbreeding depression as a result of subspecies interbreeding would be quite unlikely and the choice, therefore, of management strategy would have to be dictated by other factors such as the preservation of some desirable morphological, behavioral, or adaptive specializations.

Data on genetic variation as assessed by the finest level of resolution, that is DNA sequencing, was presented by Dr. Amato. He described the merits of the powerful and versatile polymerase chain reations (PCR) and its application to rhino genetics. DNA sequence information generated by analysis of PCR amplified products from the 12S and 16S ribosomal genes of the mitochondrial genome was used to construct phylogenetic trees for four species of the rhino using the cow or zebra as outgroups. The phylogenies strongly supported the monophyly of the African species. Both the Sumatran and Indian rhinos separated as another branch with a distant lineage split. Dr. Amato also described a new technique called RAPD (random amplified polymorphic DNA markers) that seems to hold better promise in paternity and pedigree analysis in rhinos than the conventional DNA fingerprinting techniques. The technique also has the advantage that there is no need for Southern blotting and hybridization with radioactive probes in generating data.

That techniques developed in other scientific disciplines can be applied to resolve zoogeographical separation in genetics was demonstrated by Dr. van der Merwe. He presented data on the measurements of light stable isotopes such as S, C, H, O, and N in specimens of rhino horn to determine the species of rhino that the sample originated from and its geographic origin. Carbon isotope ratios ($^{13}C/^{12}C$) are sufficient for species identification because of the natural differences in this ratio in the vegetation types that the two species of African rhino feed on, i.e. browse vs. grasses. Analysis of $^{13}C/^{12}C$ ratios in horn material from the two African rhino species resulted in an unequivocal identification of the species. Identification of the geographic origin, however, is more complex and requires multiple analysis of isotope ratios including $^{15}N/^{14}N$ (which correlates with rainfall) and heavy isotope ratios of Sr, Pb, and Nd (which register the age of geological substrate). Multivariate cluster analysis of these isotopes ratios was found to separate the geographic refuges with very little overlap, thereby identifying the geographic origin of the sample.

Plenary II - Summary
Biology and Conservation of the Greater One-Horned Rhinoceros

E. Dinerstein, chair: *Demographic characteristics of greater one-horned rhinoceros populations*
Sunder P. Shrestha: *The role of translocation of greater one-horned rhinos in species conserva-tion: The Bardia Park example*
G. McCracken: Genetic variation *in the greater one-horned rhino and implications for population structure*
Satya Priya Sinha: *Management of the reintroduced great one horned rhinoceros (Rhinoceros unicornis)in Dudwa National Park, Uttar Pradesh, India*

This session took a conservation biology approach to the management of this species. We first looked at some of the demographic considerations of this population which have been under study over the last few years and found that the Chitwan and Kaziranga populations (essentially the only viable population at the moment) had made significant recovery since the early 1900s, when they were down to very low levels. In the case of the Kaziranga population, its numbers decreased to less than a hundred individuals; for the Chitwan population, the low point was between 60 and 80 individuals in 1962. These rhino populations are an example of how adequate protection and sufficient habitat can lead to recovery.

In looking at the genetics of this population a rather startling and interesting discovery was made. The average heterozygosity in greater one-horned rhinoceroses approaches the highest levels recorded for free-ranging mammals. Gary McCracken explained how, through the historical demography of this species, genetic diversity might have been maintained in spite of the population bottleneck. The speakers in this session also recognize that the remnants of a population almost going extinct may still carry high levels of genetic variability, and that the next step in any effort to conserve the species is to reestablish these populations within the historic range of the species, particularly in areas that are now well protected and where there is adequate habitat.

Dr. Shrestha from Nepal and Dr. Sinha from Uttar Pradesh gave examples of where translocations have begun. In the very successful reintroduction and translocation of rhinoceros from Chitwan the population at Bardia is now up to 38 individuals. There have been five births. Of the first installment of rhinos that were sent there in 1986, all those born were from females that were bred in national parks, rather than females that arrived pregnant. Dr. Sinha reported on a different, opposing scenario involving the Dudwa Sanctuary population for which it appears unlikely at the moment there is enough habitat within the Dudwa Sanctuary to support a viable population.

There are a number of other areas within the historic range of the greater one-horned rhinoceros that are available for future translocation efforts. From Dr. Shrestha's work it is clear that the technology is available for the translocation of animals and a high success rate may be anticipated, unlike some of the problems we heard about with black rhinos. Thus, the translocations should become a very important part of the conservation activities for *Rhinoceros unicornis*.

Plenary III - Summary
African Rhino Status and Conservation Plans

C. Gakahu, chair: *African rhinos: Current numbers and distribution*
R. Brett: *The management of rhinos in sanctuaries in Kenya*
P.M. Brooks: *Conservation plan for the black rhinoceros in South Africa, the TBVC states and Namibia*
K.H. Smith: *Conserving rhinos in Garamba National Park*
M. Atalia: *Strategies for the conservation of rhino in Zaire*
N. Steele: *Development and management of rhino sanctuaries in South Africa: The effects of socio economic and political changes in Southern Africa on developments*

1. Numbers, distribution, and whether the trend of population(s) is decreasing, stable, or increasing in sanctuaries, nations, or regions are the basis of assessing status and therefore, vital data for management and conservation of rhinos. The databases for rhino populations should progress toward continuous monitoring of births and deaths, including, when possible, the identification of individuals. A permanent and centralized database should be established.

2. The required field surveys and monitoring are expensive and require finance, personnel, and equipment. These requirements must therefore be used rationally for max output. Finance and equipment are a major problem and assistance is required. Efforts should therefore be concentrated in areas with significant (viable) numbers of rhinos.

3. Sanctuaries offer great hope and future for rhinos, but they must be actively managed and supported by long term intensive monitoring of all aspects including vegetation, food and nutrition requirements, genetics, and disease together with physiology and veterinary needs especially for capture and translocation.

4. Objectives of conservation of rhinos can only be achieved through the implementation of co-ordinated management programs involving management of existing populations, establishment of new populations and support for captive breeding programs.

5. The main factors likely to affect the future of African rhinos ranked in order of importance are poaching, civil unrest from within and outside national boundaries, habitat changes, genetics, and inbreeding in relation to the demographic data.

6. When discussing, developing strategies and conservation plans, the socio-economic and political factors must never be underestimated. The basic survival needs of people who shoulder the cost of supporting wildlife should be catered for by the conservation programmes. Their active participation through education, understanding of benefits from wildlife (rhino included), extension and community based conservation is vital for sustained management of the natural resource base which rhinos are part of. This is both a short and long term strategy and it should not be above the most urgent and, hopefully, short term security enhancement for rhinos in sanctuaries, private lands, and government conservation areas.

Plenary IV - Summary
Captive and Other Managed Populations

P. Spala, chair: *Breeding experience with northern white rhinos*
J. Anderson: *Management of translocated white rhino in Southern Africa*
C. Furley: *The management of black and Sumatran rhinos at Port Lympne Zoopark, U.K.*
R. Reece: *Captive breeding of rhinoceroses in North America*
R. Rieches: *Rhinoceros breeding at the San Diego Wild Animal Park*

Some aspects of captive breeding of black, white, Indian and Sumatran rhino populations were discussed with the following results:

1) None of the captive rhino programs have so far reached the sustaining level.

2) The southern white rhino groups have not proved to be growing at expected rate. The other SSP's for rhinos are progressing satisfactorily.

3) Fulfillment of required population size objectives will require a doubling of available space.

4) Disease factors appear more prominent in browsing species (i.e., black rhino) than in grazing ones.

5) More research in reproduction, genetics, behavior, nutrition, etc., is necessary to achieve self-sustaining populations.

6) Managed populations of the translocated white rhinos in Southern Africa are doing well and are currently producing surplus at the rate of 10% per year.

Plenary V - Summary
Endocrinology and Reproduction

J.K. Hodges, chair: *Studies in rhinoceros reproductive endocrinology*
N. Czekala: *Salivary hormone analysis for black rhino pregnancy detection*
R. Godfrey: Progress in reproductive physiology researcy in rhinoceros
J. Hindle: *Recent advances in reproductive monitoring of rhinos in captivity and in the wild*
N. Schaffer: *Reproductive ultrasound and semen collection in chute-restrained cognizant rhinoceroses*

The aim of the session was to provide a brief account of current status in the field of reproductive physiology and to examine priorities for future studies in relation to management/conservation needs. Keith Hodges provided some background on the importance of monitoring methods, different approaches and potential applications. Jo Hindle highlighted the species differences hormone metabolism and their implication for methods of urinary hormone analysis. She presented data describing the pattern of excretion of 20α-dihydroprogesterone (20α-HP) and conjugated estrogens, allowing for the first time the monitoring of follicular development and corpus luteum function in African rhinos. An alternative method of monitoring based on hormone analysis of saliva was described by Nancy Czekala. The measurement of 20α-HP and estrogens in saliva should be useful in pregnancy diagnosis and prediction of parturition in the black rhino. Data on circulating levels of estradiol and progesterone during the ovarian cycle in a black rhino were presented by Bob Godfrey, showing that animals may be trained to use a squeeze chute for non-stressful blood sampling. He also reported that ovarian follicles, a corpus luteum and an early embryo had been visualized in using ultrasound. Nan Schaffer summarized her work on ultrasound and reproductive tract gross anatomy. The finding of a convoluted cervix may cause difficulties when attempting intra-uterine insemination. She also reported that viable semen had been collected from epididymes and by electrical and manual stimulation from Indian and African rhinos.

The value of assisted reproductive technologies (A.I., embryo transfer) to rhino management was discussed. Potential was clearly seen for captive animals. However, much more work was needed and any real impact on rhino conservation is unlikely within the next five years.

Priorities for the future.

1. Confirm endocrine data for ovarian cycle in African rhinos. More cycles from more animals are needed (especially white).

2. Correlate urinary data with blood samples and ultrasound. Focus on timing of ovulation and assessment of luteal function.

3. Greater precision is required for hormonal profiles during (early) pregnancy. The range of normal values for urinary and salivary hormones needs to be established.

4. Alternative methods of early pregnancy diagnosis need to be sought.

5. Method of pregnancy diagnosis from 1 or 2 samples needs to be developed to facilitate use on free-ranging animals.

6. Use of faecal hormone analysis for pregnancy detection should be pursued (due to potential for use with wild animals).

7. Wherever possible squeeze chute (crush) facilities should be installed and animals conditioned to regular handling.

8. Methods for ovarian stimulation and synchronization of ovulation need to be established. Different approaches, doses, treatment protocols and responses all need to be worked out.

9. Success rate for semen collection needs to be improved. Further work is needed to establish optimal semen freezing and storage methods. Procedures and instumentation for A.I. need to be developed.

10. Placental material (particularly early pregnancy) should be collected and stored for structural, histological and endocrine evaluation.

Plenary VI - Summary
Biology and Conservation of Sumatran and Javan Rhinos

Mohd. Khan, chair: *Conservation planning for the Sumatran rhinoceros*
C. Santiapillai *Conservation and management of Javan rhino (Rhinoceros sondaicus) in Vietnam*
K. MacKinnon: *Conservation and management of Sumatran Rhino (Dicerorhinus sumatrensis) in Indonesia*
Sukianto Lusli: *The status of Sumatran Rhino Rescue Programme in Indonesia*
Widodo Ramono: *Conservation and management of Javan rhino (Rhinoceros sondaicus) in Indonesia*
Linda Prasetyo: *Sumatran rhino (Dicerorhinus sumatrensis) captive propagation in relation to its conservation*

(Plenary session summary not available at this time)

Indonesian Rhino Conservation Informal Meeting

An informal meeting was conducted to exchange information and ideas relative to rhino conservation in Indonesia.

In particular, the group discussed plans and preparations for the Indonesia Rhino Conservation Workshop that had been postponed last January and is now to occur 3-5 October 1991 in Bogor, Indonesia. The draft agenda for this Workshop was reviewed and revised. Major items on the agenda include a review of the PVA process for Javan rhino, the Global Heritage Species Programme proposal for Sumatran Rhino, and the Indonesian Rhino Conservation Action Plan. Also reviewed was the Briefing Book being prepared for this Workshop. Numerous recommendations and materials were submitted for addition.

Also distributed and discussed were:

The latest draft Studbook for Sumatran Rhino including more refined analyses of the mortality that has occurred during the program.

The second draft of the Prototype Action Plan for Sumatran Rhino as a Global Heritage Species Programme.

Further PVA Analyses using VORTEX software from R. Lacy as well as an alternative approach developed by H. Prins. Directions for additional analyses before the October Workshop were explored.

The meeting concluded with an agreement by those attending to continue dialogue in preparation for the October Workshop to maximize the productivity of that meeting.

Summary of Global Propagation Group Meeting - Sumatran Rhino

The first meeting of the Global Propagation Group for the Sumatran Rhino was convened in conjunction with the International Rhino Conference in San Diego. In attendance were representatives of the 4 countries and 8 of 11 facilities maintaining captive specimens.

The purpose of the session was to review and advance the captive propagation program as part of the conservation strategy and action plan for this species. Studbook Keeper Foose presented a summary of the program since 1984.

31 (12/19) rhino have been captured in the 3 regions where rescue operations are being conducted: Indonesia 15 (6/9); Peninsular Malaysia 11 (2/9); Sabah 5 (4/1).

9 (4/5) rhino have died from a variety of causes which were reviewed; mortality has been differential in the various regions and facilities; death rates have declined over history of the program; last death occurred in 1989.

One animal has been born in captivity although conceived in the wild.

23 (8/15) rhino are alive in captivity today in 5 countries and 11 facilities: Indonesia 7 (3/4) rhino at 4 sites; Peninsular Malaysia 7 rhino (1/6) at 2 sites; Sabah 3 (2/1) rhino at 1 site; U.K. 2 rhino (1/1) at 1 sites.

Reproduction has been impeded by dearth of mature males.

An institution and animal by animal review of the captive population was conducted. Representatives of the 3 regions described their plans to optimize reproductive opportunities for rhino. Breeding activity was described in the U.K. and Jakarta where apparently full copulations have been observed. Plans were discussed to place male with females on regular basis in new Sungai Dusun Rhino facility in Peninsular Malaysia which will also now resume attempts to capture additional rhino especially males. U.S. representatives discussed plans to place all 3 females with the available male over next year.

Parties agreed to intensify efforts to investigate subspecies distinctions among rhino from different regions to guide reproductive programs. Amato offered his laboratory without qualification for this effort. A research working group was also organized to facilitate and improve cooperation and coordination among scientists in the several countries.

Finally, a prototype proposal to employ the species as an umbrella and perhaps Heritage Species was presented.

Parties agreed to continue dialogue and collaborations at October Rhino Workshop in Indonesia.

Plenary VII - Summary
Strategic Planning for Rhinoceros Conservation

R. Martin, chair: *Development of the Zimbabwe national conservation strategy for black rhinocerso*
T.J. Foose: *Global management of rhinos*
N. Leader-Williams: *Theory and pragmatism in the conservation of rhinos*

All these papers recognized a average minimum recurrent cost of US $200/sq. km. to conserve wild rhinos *in situ*. Martin showed data which indicated that this could rise to $400/sq km under conditions pertaining in Zimbabwe. Foose used these figures to estimate *in situ* conservation costs for viable populations of all taxa of rhino at $20-40 million per year.

All three speakers agreed that it was necessary to meet threshold funding (and manpower) levels to prevent failure of *in situ* conservation efforts. With current funds available for conservation this inevitably implies a departure from attempts to conserve rhinos in very large areas and an emphasis on smaller units dictated by budgets. Programs in Zimbabwe and other countries have incorporated this feature by focussing additional manpower in designated zones to protect large wild populations.

Thereafter there was some divergence of opinion among the speakers on the most effective approach for conservation action. In his presentation of a global strategy, Foose placed emphasis on the conservation biology aspects of rhino populations which were either dangerously close to or below viable population levels. He saw the future for rhinos lying in managed metapopulations consisting of *in situ* subpopulations and *ex situ* captive breeding subpopulations between which controlled movement of breeding animals would be necessary to maintain genetic diversity and demographic security. Highest priority should be placed on increasing both wild and captive bred populations immediately to escape deleterious stochastic threats. Foose felt that the situation had reached a stage where it was undesirable that any taxa of rhino should be reliant on a single political authority for its survival. While advocating the value of captive breeding programs, Foose observed the need for improvement in husbandry.

Leader-Williams presented a powerful case that the <u>only</u> effective conservation of rhinos to date had occurred *in situ* in areas where adequate budgets and manpower had been provided. He presented data to show that, to date, the contribution of *ex situ* captive breeding programmes to conservation of rhinos (and several other species) had been negligible and costly. He expressed caution at experimenting with captive breeding at a stage when many populations needed immediately to be increased to more secure levels.

Martin, also, felt that *in situ* protection of rhinos was of the utmost priority. He highlighted the fact that adequate budgets for such efforts could be obtained sustainably within the three southern African countries which now contain over 90% of Africa's black and white rhinos by taking advantage of the inherent economic value of rhino. A controlled trade in legal government stocks of rhino horn and/or the raising of revenues from a small quota of animals for sport hunting could provide the necessary funds. Current contributions to rhino conservation from the international community were small compared to the budgets allocated by those African governments who had achieved successful conservation of rhino, and these governments sought to remain self-sufficient in funding through sustainable conservation measures. Zimbabwe had made a secondary commitment to *ex situ* captive breeding by its intent to provide a viable founder population of black rhino. It saw this as an ultimate form of insurance in the very long term against extinction possibilities but did not in any way view this as reducing the *in situ* conservation requirements.

In summary:

1. The paramount goal should be the maintenance or restoration of viable wild rhino populations.
2. More money needs to be directed toward this effort either by greater donor involvement or by sustainable utilization of the species including the use of its high economic value.
3. Captive propagation could offer an ultimate insurance against extinction provided that better husbandry, management, and breeding performance can be achieved.

Plenary VIII - Summary and Working Group Report

Health, Disease, Nutrition and Pharmacology: Veterinary Aspects of Rhinoceros Conservation

E. Miller, chair: *Health concerns and veterinary research in the North American black rhinoceros (*Diceros bicornis*) population*
C. Furley: *Diseases and management of black and Sumatran rhinoceroses at the Howletts and Port Lympne zoos*
L. Geldenhuys: *Capture and translocation of black rhino in Namibia*
D. Jessup: *Health data gained from black rhinoceroses immobilized for relocation*
M. Kock: *Capture and translocation of the black rhinoceroses (Diceros bicornis) in Zimbabwe: Management modifications to reduce stress and mortalities*
R. Kock: *Veterinary management of three species of rhinoceroses in zoological collections*
R. Montali: *Pathological findings in captive rhinoceroses*
P. Morkel: *Translocation and dehorning of wild black rhinoceroses*
L. Munson: *Mucosal and cutaneous ulcerative syndrome in black rhinocerso (Diceros bicornis)*

In view of the role that health and nutritional problems in the maintenance of captive rhinoceros populations (eg. as a limiting factor in the growth of the captive black rhinoceros population), and that they have presented concerns in wild populations and their translocations, the following points for consideration and action are recommended:

1. Continued investigation of health problems in wild and captive rhinoceroses. New and continued research should be organized and encouraged in the following areas:

All morbidity and mortality data from captive, and where possible, wild populations should be compiled and reviewed annually under the auspices of the regional species management plans and national wildlife programs, and those regional data reviewed under the auspices of the IUCN/CBSG Rhinoceros Action Plan. Such studies should include evaluation of post-capture and post-translocation mortalities.

Investigation of fertility and the incidence and prevention of management related disease and trauma.

Additionally, monitoring the fertility of all rhinoceros populations with particular attention to fertility in Indian rhinoceroses and abortion rates in black rhinoceroses.

Enhancement of baseline data for normal values from free-ranging and captive rhinoceroses of all species is of critical importance to all fields of research.

Epidemiology of health problems in captive and wild rhinoceros populations and comparison of patterns in each. Such research should include seroprevalence surveys for infectious diseases and evaluation of internal and external parasites and their health significance.

Continued sharing and refinement of immobilization regimens between wildlife and zoo veterinarians should take place. Narcotic agents (etorphine and carfentanil) are the primary drugs used for immobilization, and further investigations are needed to establish preferable supplemental tranquilizers, particularly long-acting neuroleptic agents.

Metabolic consequences of anesthesia and the stresses associated with capture and the sequelae of both should be assessed.

Studies to address the immunocompetency of wild and captive black rhinoceroses and the role that immunology may play in several of their diseases, eg, fungal pneumonia of black rhinoceroses.

Nutritional research should include general review of the feeding practices used in all species in captivity with particular attention to minimal requirements. Basic nutritional evaluations should focus attention on both the nutrition of wild and captive populations. Research to establish effective dietary supplementation with α-tocopherol should be encouraged.

In black rhinoceroses further research should be designed to evaluate the following diseases and syndromes:

Hemolytic anemia - Current recommenda-tions for the prevention of acute hemolytic anemia include vaccination of captive animals with a bacterin containing 5 leptospiral serovars. Research to an underlying cause for the hemolysis should continue.

Oral/skin ulcers

Further evaluation of iron metabolism due to the accumulation of hepatic iron in captive and newly captured black rhinoceroses.

Fungal pneumonia

Encephalomalacia.

2. In conjunction with the above proposals, identification of additional funding resources to support health research in rhinoceroses is vital.

3. Continued maintenance and enhanced participation in regional biomaterial banks (tissue, sera, urine, etc) with materials from both captive and wild rhinoceroses of all available species is vital to future comparative studies.

4. Continued and enhanced collection of genetic samples from anesthetized animals whenever possible.

5. Continued and improved communication between veterinarians working with both wild and captive rhinoceroses should be enhanced through future meetings. Special effort should be applied to the maintenance of continuous medical histories for rhinoceroses translocated from the wild to captivity.

In summary, there should be veterinary participation in the management of captive and wild rhinoceros populations. This participation should be an integral part of a multidisciplinary approach to their care, and is particularly relevant to their capture and translocation. Such efforts will contribute to the long term survival of both *in situ* and *ex situ* rhinoceros populations.

Planning for Rhinoceros Conservation

Proposed consensus items and/or issues for discussion and clarification:

1) There should be a greater flow of funds from international development agencies to projects that conserve biological diversity.

2) There is a need for increased flow of information concerning the costs of *ex situ* and *in situ* conservation.

3) There is a need for more accurate and timely reporting of data concerning population abundance, especially for *in situ* populations of black, Sumatran and Javan rhino.

4) Civil and military conflicts within and between nations pose a proximate threat to rhino populations.Demographic vulnerability due to small population size poses the most immediate threat to wild populations of rhinos where poaching activities are under control and where negative civil and military impacts on rhino populations are precluded.

5) A closer examination of husbandry regimes for rhinos in zoological parks is warranted in order to gain insights into their apparently less-than-maximal reproduction rates.

6) Non-invasive reproductive monitoring of rhinos in zoological parks should be expanded and, as possible, compared with data obtained from *in situ* sanctuary and *ex situ* sanctuary populations of rhinos.

7) The development of a simple pregnancy test, especially one that could be employed under field conditions would be of use in both *in situ* and *ex situ* management of rhinos.

8) It is worthwhile at this time to conduct experiments in the introduction of black rhinos into existing populations. The existing populations should be derived from demographically and genetically secure sources so that their reproduction is not considered essential for meeting gene pool conservation goals in the region. The introduced rhinos could include individuals of either sex and be derived from zoological parks or *in situ* populations. (i.e., it is valuable now to begin to develop successful approaches for the creation of metapopulations).

9) A Second International Conference on Rhinoceros Biology and Conservation is warranted as in three years' time new information on disease, reproduction and the development of sanctuary programs is anticipated.

Working Group Report Conservation of the Northern white rhinoceros

Ceratotherium simum cottoni

At the International Conference on Rhinoceros Biology and Conservation the most recent information available was exchanged. A Northern white rhinoceros working group met and presented their report at a conference plenary session.

Recommendations are made in three areas: conservation of the *in situ* population, conservation of the *ex situ* population, and coordination of these efforts.

In situ population

The success of the conservation efforts for the Northern white rhinoceros in Garamba National Park taken by the government of Zaire is recognized and those responsible are to be commended for their actions.

Continuation or increase in the levels of international funding for the Garamba ecosystem and an increase in the level of research efforts in support of the Northern white rhinoceros is recommended.

External assistance is recommended for the further training of park staff in techniques of wildlife protection.

Further research should be undertaken on nutrition and feeding ecology. Research should also be undertaken on the genetic status of the Garamba population. Collection of samples for genetic analyses, including examination of the levels of genetic diversity and in methods of parentage determination, should be encouraged. Research should be initiated on the role of infrasonic vocalizations in communication between and among individual rhinos in the park.

Research findings on the rhinos in Garamba Park can usefully support investigations into reproductive efficiency of the captive population and *vice versa*. The detection of pregnancy, especially of the early stages of pregnancy, would have useful application to the Garamba Northern white rhinoceros.

Ex situ population

Recommended is the aggressive investigation of the estrus cycles and continuous monitoring of all captive females (except those less than 5 years of age). Monitoring of salivary and/or urinary 20α-DHP and estrogen conjugates is recommended.

Semen collection and freezing from all males should be undertaken.

A technical working group should be convened to discuss the options and protocols for the most appropriate action to be undertaken in order to increase the reproductive potential of the *ex situ* population.

The feasibility of induction and/or synchronization of estrus should be investigated using female Southern white rhinos.

All zoological parks maintaining Northern white rhinoceros should immediately construct and install manipulation chutes that allow for the safe handling of animals for reproductive examinations and other necessary veterinary investigations. Plans are available for these manipulation chutes.

The zoological parks that hold the Northern white rhinoceros have a critical responsibility for these animals and their potential contribution to the gene pool. The activities of these institutions should be monitored by the IUCN Captive Breeding Specialist Group. The individual rhinos removed from the wild provide a crucial source of gene pool resources that are of potential benefit to the future of the wild population.

No further transfers of Northern white rhinoceros from the Zoo Dvur Kralove is recommended at this time. The collection of a breeding nucleus of the Northern white rhinoceros and its husbandry at Dvur Kralove enable the option of utilizing an *ex situ* population in support of the population in the wild and the ecosystem in which it exists.

Coordination of efforts for *in situ* and *ex situ* conservation

More frequent and detailed communication of data and research conclusions is recommended. Detailed summaries of information relevant to reproduction and population management should be exchanged between all parties.

The opportunities for cooperation and linkage of aspects of the management of the gene pool resources is recognized by all parties and efforts to develop appropriate approaches to linking *in situ* and *ex situ* populations should be explored.

CURRENT RHINO POPULATIONS AND DISTRIBUTION

Introduction - The following represents the most current data available on rhinoceros populations and their distribution. It was collected by personal interview, conference presentations and related materials gathered at the International Symposium on Rhinoceros Biology and Conservation held May 9 through May 11 in San Diego, California, USA.

Northern White Rhinoceros - the Northern White rhinoceros *(Ceratotherium simum cottoni)* currently exists in the wild only in Garamba National Park, Zaire. The population there consists of 15 males and 13 females (K.H. Smith, 1991); six of these males and twelve of the females form the actively breeding portion of the population.

The captive population resides in two institutions: Vychodoceska Zoo in Dvur Kralove, Czechoslovakia and the Wild Animal Park in San Diego, USA. The Vychodoceska Zoo has two males and five females. One of the females is a Northern White/Southern White hybrid (P. Spala 1991). The Wild Animal Park has two males and two females in its herd.

Southern White Rhinoceros - the status of the Southern White rhinoceros *Ceratotherium simum simum* in the wild over the past decade is as follows (from C.G. Gakahu, 1991 and with revisions):

	1980	1984	1990
Botswana:	70	200	15
CAR:	20	1	0
Kenya:	25	30	65
Mozambique:	30	20	0
Namibia:	150	70	200
South Africa:	2500	3330	4225
Swaziland:	60	60	8
Zambia:	5	10	6
Zimbabwe:	180	200	200
	3841	3947	4745

The captive population consists of 698 individuals (342 males, 355 females one undetermined) in 245 institutions according to the 1991 African Rhino Studbook.

Black Rhinoceros - the status of the Black rhinoceros *(Diceros bicornis)* in the wild over the past decade is as follows (from C.G. Gakahu, 1991):

	1980	1984	1987	1990
Angola:	300	90	0	0
Botswana:	30	10	10	2
Cameroon:	110	110	25	15
CAR:	3000	170	10	0
Chad:	25	5	5	2
Ethiopia:	20	10	0	6
Kenya:	1500	550	520	400
Malawi:	40	20	25	5
Mozambique:	250	130	0	0
Namibia:	300	400	470	400
Rwanda:	30	15	15	9
Somalia:	300	90	0	0
South Africa:	630	640	580	626
Sudan:	300	100	3	0
Swaziland:	0	0	0	2
Tanzania:	3795	3130	270	185
Uganda:	5	0	0	0
Zambia:	2750	1650	110	40
Zimbabwe:	1400	1680	1760	1700
	14,785	8800	3803	3392

The captive population, according to the 1991 African Rhino Studbook, consists of 91 males and 113 females (204 total animals) in 72 institutions.

Greater One-Horned Rhinoceros - the Greater One-Horned rhinoceros *(Rhinoceros unicornis)* is known in the wild in the following locations (from the Action Plan: Asian Rhino Specialist Group (1989), Dinerstein (1991), Sinha (1991)):

INDIA-	
Manas (Bhutan border):	60
Dudwa:	9
Kaziranga:	1080
Laokhowa:	5
Orang:	65
Pobitara:	40
Pockets in Assam:	25
Pockets in West Bengal:	32
NEPAL-	
Royal Bardia:	38
Royal Chitwan:	358
PAKISTAN -	
Lal Sohanra:	?
TOTAL =	1712

The captive population currently consists of 67 males and 47 females (114 total individuals) in 43 institutions.

Javan Rhinoceros - there are between 52 and 62 Javan rhinos *(Rhinoceros sondaicus)* currently in Ujung Kulon, Java, Indonesia (Ramono, 1991). The Vietnamese population is estimated at 8 to 12 individuals (Santiapelli, 1991) in the area where the Song Be, Lam Dong, Dong Nai and Dac Lac regions meet.

Sumatran Rhinoceros - *Dicerorhinus sumatrensis* is distributed in the following areas in Southeast Asia (Khan, 1989 & 1991):

BURMA -	
Schwe-u-daung:	?
Tamanthi:	?
Burma:	6-7
INDONESIAN BORNEO (Kalimantan) -	
near Sabah border:	30
SUMATRA, INDONESIA -	
Gunung Leuser:	130-200
Gunung Patah:	?
Kerinci Seblat:	250-500
Gunung Abong-abong & Lesten-Lukup:	15-25
Berbak:	?
Torgamba:	?
Barisan Selatan:	25-60
PENINSULAR MALAYSIA -	
Endau Rompin:	10-25
Taman Negara:	26-40
Sungai Dusun:	3-4
Gunung Belumut:	3-5
Mersing Coast:	5-6
Sungai Depak:	2-4
Sungai Yong:	3-5
Kuala Balah:	2-4
Bukit Gebok:	2
Krau Reserve:	1
Sungai Lepar:	2
Ulu Atok:	1
Ulu Selama:	11
Ulu Belum:	2-4
Bubu Forest:	2
Kedah:	5
Between Ulu Selama & Kedah:	2-3
MALAYSIAN BORNEO-	
Tabin Reserve, Sabah:	20+
Kretam/Dent Peninsula, Sabah:	8
Danum Valley, Sabah:	10
Limbang, Sarawak:	13
THAILAND-	
Phu Khieo:	?
Tenasserim Range:	6-15
Khao Soi Dao Reserve:	?
TOTAL =	595-1012

The captive population currently stands at 19 rhinos (6 males and 13 females) in 9 institutions and two (one male, one *female*) at the Ipuh capture site (Draft Sumatran Rhino Studbook, 1991).

INDONESIAN RHINO CONSERVATION WORKSHOP

BRIEFING BOOK

SECTION 10 - POPULATION & CONSERVATION BIOLOGY

INTRODUCTION

An endangered species is (by definition) at risk of extinction. The dominant objective in the recovery of such a species is to reduce its risk of extinction to some acceptable level - as close as possible to the background, "normal" extinction risk all species face.

The concept of risk is used to define the targets for recovery, and is used to define recovery itself. Risk, not surprisingly, is a central issue in endangered species management. Unfortunately, there is ample reason to suppose that we (as humans) are not "naturally" good at risk assessment. Recovery will be more often successful if we could do this better. There is a strong need for tools that would help managers deal with risk. We need to improve estimation of risk, to rank order better the risk due to different potential management options, to improve objectivity in assessing risk, and to add quality control to the process (through internal consistency checks). Among the risks to be evaluated are those of extinction, and loss of genetic diversity.

In the last several years such tools have been developing. The applied science of Conservation Biology has grown into some of the space between Wildlife Management and Population Biology. A set of approaches, loosely known as "Population Viability Analysis" has appeared.

These techniques are already powerful enough to improve recognition of risk, rank relative risks, and evaluate options. They have the further benefit of changing part of the decision making process from unchallengeable internal intuition to explicit (and hence challengeable) quantitative rationales.

In the following sections, Tom Foose, Bob Lacy, and Jon Ballou each describe aspects of Population Viability Analysis (PVA). The text, adapted from that used in other PVAs (Ballou et al. 1989, Lacy et al. 1989), provides an overview of some of the population biology concepts that form the foundation of Population Viability Assessment. Each contributor approaches the subject from their own expertise and experience, so the contributions differ somewhat in perspective and content. There is some overlap, which may help the newcomer by occasionally repeating a point in different language. After these general reviews, information on the captive and wild populations of the Javan and Sumatran rhinoceroses to provide a basis for a detailed PVA is presented, and recommendations for improving the probability of recovery of the taxon.

SMALL POPULATION OVERVIEW (J. Ballou)

The primary objective of single-species conservation programs is to reduce the risk of population extinction. A first step in doing this is to identify those factors that can potentially cause extinction in the population. The most fundamental threat is, of course, declining population size. If a population is declining in numbers, and no action is taken to reverse the trend, then extinction is imminent. However, if the population is not declining, its fate is less certain and predicting its future more complicated.

The foremost problem facing the conservation of small populations is that these populations are still highly vulnerable to extinction even through they may be maintaining their size or even increasing in number. Small populations are challenged by a number of factors that increase the likelihood of the population going extinct simply because the population is small.

CHALLENGES TO SMALL POPULATIONS

Challenges to small populations can be roughly categorized as demographic and/or genetic in nature. Beginning with demographic challenges, at the most basic level, the level of the individual, the population is threatened by Demographic Variation. Demographic variation is the normal variation in the population's birth and death rates and sex ratio caused by random differences among individuals in the population. The population can experience fluctuations in size simply by these random differences in individual reproduction or survival. These randomly caused fluctuations can be severe enough to cause the population to go

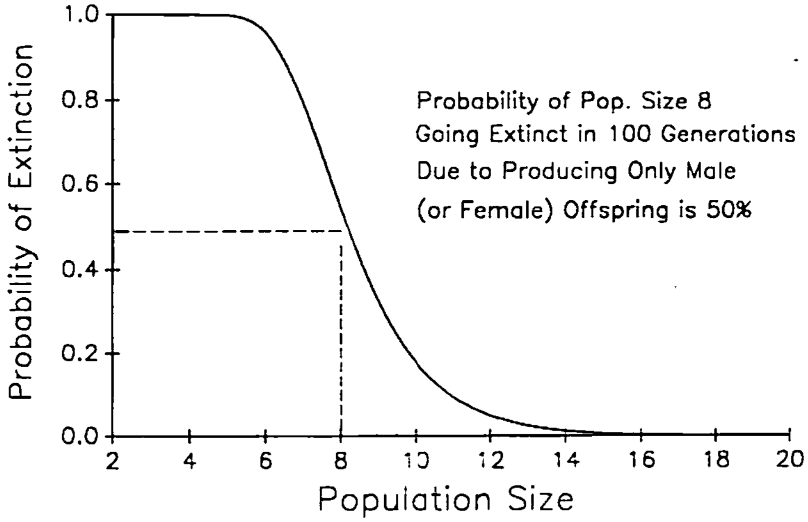

Figure 1. Example of demographic variation: Probability of extinction by 100 generations due solely to producing only one sex of offspring during a generation.

extinct. For example, one concern in extremely small populations is the possibility that all individuals born into the population
during one generation are of one sex, resulting in the population going extinct. Figure 1 illustrates the probability of this occurring over a 100 generation period in populations of different size. There is a 50% chance of extinction due to biased sex ratio in a population of size 8 sometime during this time period.

Similar consequences could result from the coincidental effects of high death rates or low birth rates. However, these risks are practically negligible in populations of much larger size. In general, the effect of any one individual on the overall population's trend is significantly less in large populations than small populations. As a result, demographic variation is a relatively minor challenge in all but very small populations (less than 20 animals).

A more significant threat to small populations is Environmental Variation. Variation in environmental conditions clearly impact the ability of a population to reproduce and survive. Populations susceptible to environmental variation fluctuate in size more than less susceptible populations, increasing the danger of extinction. For example, reproductive success of the endangered Florida snail kite (Rostrhamus sociabilis) is directly affected by water levels, which determine prey (snail) densities: nesting success rates decrease by 80% during years of low water levels. Snail kite populations, as a result, are extremely unstable (Bessinger 1986).

Another level of threat to small populations are Disease Epidemics and Catastrophes. Epidemics and catastrophes are similar to other forms of environmental variation in that they are external to the population. However, they are listed separately because we are just beginning to appreciate their role as recurrent but difficult to predict environmental pressures exerted on a population. They can be thought of as relatively rare events that can have devastating consequences on the survival of a large proportion of the population. Less devastating diseases and parasites are a natural accompaniment of all species and populations that may act to decrease reproductive rates and increase mortality.

Epidemics can have a direct or indirect effect. For example, in 1985 the sylvatic plague had a severe indirect effect on the last, remaining black-footed ferret population by affecting the ferrets prey base, the prairie dog. Later that same year, the direct effect of distemper killed most of the wild population and all of the 6 ferrets that had been brought into captivity (Thorne and Belitsky 1989).

Catastrophes are one-time disasters capable of totally decimating a population. Catastrophic events include natural events (floods, fires, hurricanes) or human induced events (deforestation or other habitat destruction). Both large and small populations are susceptible to catastrophic events. Tropical deforestation is the single most devastating 'catastrophe' affecting present rates of species extinction. Estimates of tropical species' extinction rates vary between 20 and 50% by the turn of the century (Lugo 1988).

Small populations also are susceptible to genetic challenges. The primary genetic consideration is the loss of genetic variation. Every generation the genes that get passed on to offspring are a random sample of the genes of the parents. In small populations, this random sample of genes is a small sample and may be unrepresentative of the genes of the parental generation. Some of the genetic variation present in the parents, may not, just by chance, get passed on to the offspring. This genetic variation is then lost to the population. This process is called genetic drift because the genetic characteristics of the population can drift or vary over time. In small populations, genetic drift can cause rapid loss of genetic variation - the smaller the population, the more rapid the loss of variation.

Inbreeding (matings between relatives) can also cause populations to lose genetic diversity. In small populations, all the animals quickly become related; they share common alleles. Offspring produced from related parents are inbred and because the parents are related, the offspring can get the same alleles from its mother and father. Inbred individuals are therefore more homozygous than non-inbred individuals and have lower levels of genetic diversity than animals born to unrelated parents.

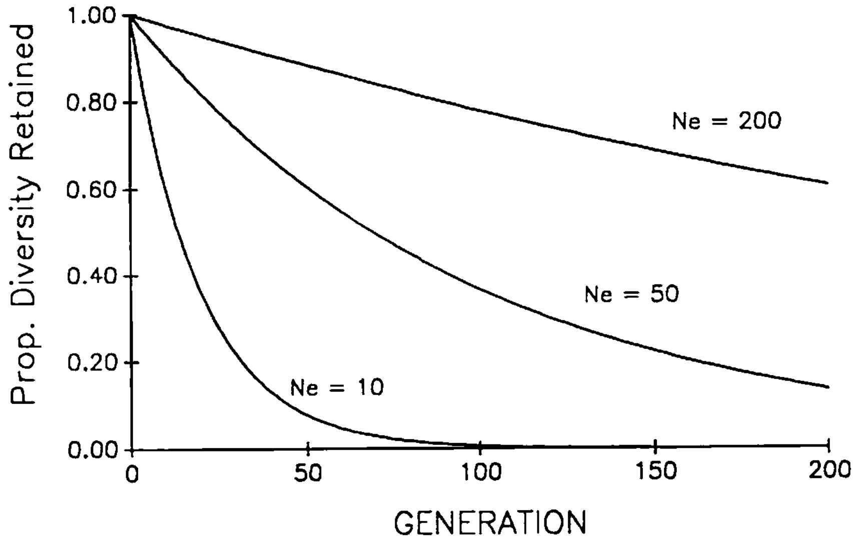

Figure 2. Loss of genetic diversity over 200 generation in populations with different effective sizes (Ne).

The loss of genetic variation in populations of different size is shown in Figure 2. The rate of loss is a function of the effective size of the population (Ne: the percent of diversity lost each generation is 1/2Ne). Technically, a population's effective size is the size of an ideal population that loses genetic diversity at the same rate as the real population. There is extensive literature on how to estimate a population's effective size (Lande and Barrowclough 1987); however, the number of animals contributing to the breeding pool each generation can be used as a very rough estimate of the effective size. The effective size of the population is therefore much less than the actual number of animals; estimates suggest that Ne is often only 10 to 30% of the total population. Seemingly large populations will lose significant levels of genetic diversity if their effective sizes are small.

Conservation programs include the maintenance of genetic diversity as a primary goal for several reasons. If species are to survive over the long-term, they must retain the ability to adapt to changing environments (i.e. evolve). Since the process of natural selection requires the presence of genetic variation, conservation strategies must include the preservation of genetic diversity for long-term survival of species. In addition to long-term evolutionary considerations, the presence of genetic diversity has been shown to be important for maintaining the fitness of the population. A growing number of studies show a general, but not universal, correlation between genetic diversity and various traits related to reproduction, survival and disease resistance (Allendorf and Leary 1986). Individuals with lower levels of genetic variation often have higher mortality rates and lower reproductive rates than individuals with more diversity.

Data on the effects of inbreeding in exotic species also show the importance of maintaining genetic diversity. Numerous studies have shown that inbreeding can significantly reduce reproduction and survival in a wide variety of wildlife (Ralls and Ballou 1983; Wildt et al, 1987; Figure 3). Inbreeding depression results from two effects: 1) the increase in homozygosity allows deleterious recessive alleles in the genome to be expressed (whereas they are not in non-inbred, more heterozygous individuals); and 2) in cases where heterozygotes are more fit than homozygostes simply because they have two alleles, the reduced heterozygosity caused by inbreeding reduces the fitness of the inbred individuals (overdominance). In both cases, the loss of genetic variation due to inbreeding has detrimental effects on population survival.

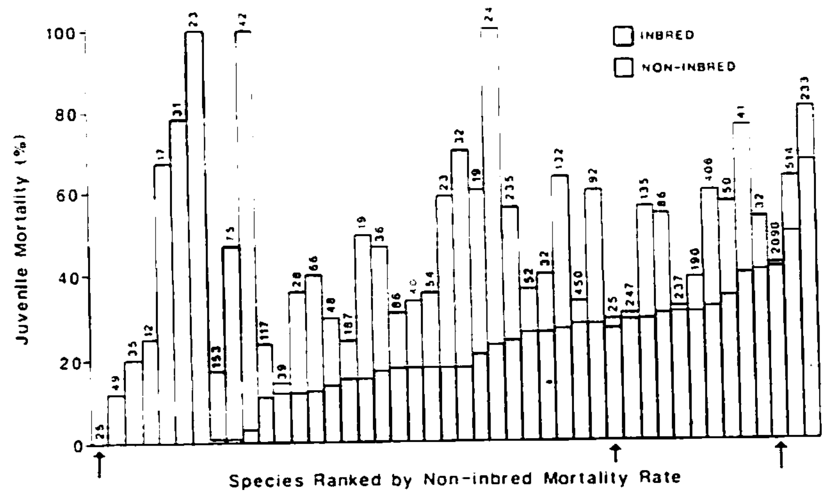

Figure 3. Effects of inbreeding on juvenile mortality in 45 captive mammal populations (From Ralls and Ballou, 1987).

Small isolated populations, with no migration from other populations, lose genetic diversity and become increasingly inbred over time. Their long-term survival potential is jeopardized since they gradually lose the genetic diversity necessary for them to evolve and their short-term survival is jeopardized by the likely deleterious effects of inbreeding on survival and reproduction.

The genetic and demographic challenges discussed above clearly do not act independently in small populations. As a small population becomes more inbred, reduced survival and reproduction are likely: the population decreases. Inbreeding rates increase and because the population is smaller and more inbred, it is more susceptible to demographic variation as well as disease and severe environmental variation. Each challenge exacerbates the others resulting in a negative feedback effect termed the "Extinction Vortex" (Gilpin and Soule, 1986). Over time the population becomes increasing smaller and more susceptible to extinction (Figure 4).

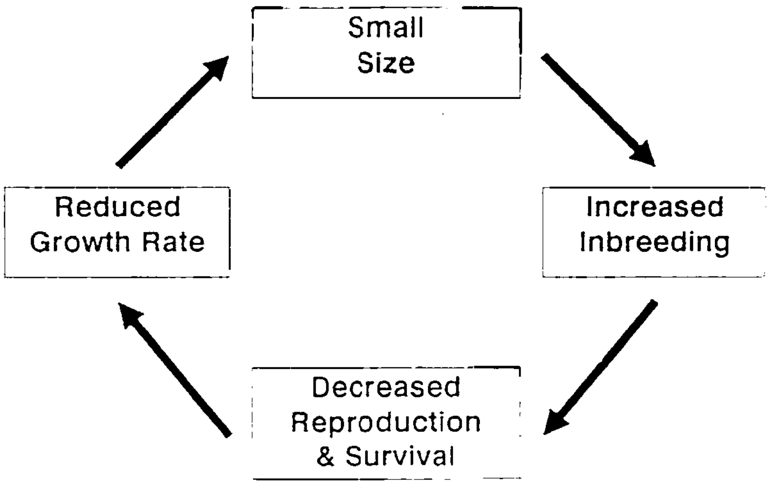

Figure 4. "Extinction Vortex" caused by negative feedback effects of inbreeding in small populations.

POPULATION VIABILITY ANALYSES

Many of the challenges facing small populations are stochastic and are result from random unpredictable events. Many can generally be assumed to decrease the likelihood of long-term survival of the population. However, because of their stochastic nature, their exact effects on population extinction and retention of genetic diversity can not be predicted with total accuracy. For example although inbreeding depression is a general phenomenon, its effects vary widely between species (Figure 3) and it is not possible to precisely predict how any one population will respond to inbreeding.

Nevertheless, conservation strategies that address these unpredictable issues of extinction and loss of genetic diversity must be developed and implemented. The process that has been developed over recent years to assess extinction probabilities and loss of genetic diversity is called Population Viability Analysis (PVA; Soule 1987). PVA is defined as a systematic evaluation of the relative importance of factors that place populations at risk. It is an attempt to identify those factors that are important for the survival of the population. In some cases, this may be easy - habitat destruction is often a critical factor for most endangered species. But at other times, the effects of single factors, and the interaction between factors, are more difficult to predict.

To try to gain a more quantitative understanding of the effect of these factors, computer models have been developed that apply a combination of analytical and simulation techniques to model the populations over time and estimate the likelihood of a population going extinct and the loss of its genetic variation. The model is first provided with information describing the life-history characteristics of the population. Depending on the model used, this includes data on age of first reproduction, litter size distribution, survival rates, mating structure and age distribution as well as estimates of the variation associated with each of these variables. A number of different external factors may also be considered. This may include levels of environmental variation, change in carrying capacity and severity of inbreeding depression. Models also allow consideration of threats facing the population: probability of catastrophes and their severity, habitat loss and disease epidemics (Figure 5). The models use the life-history variables, the external factors and the potential threats to project the population into the future.

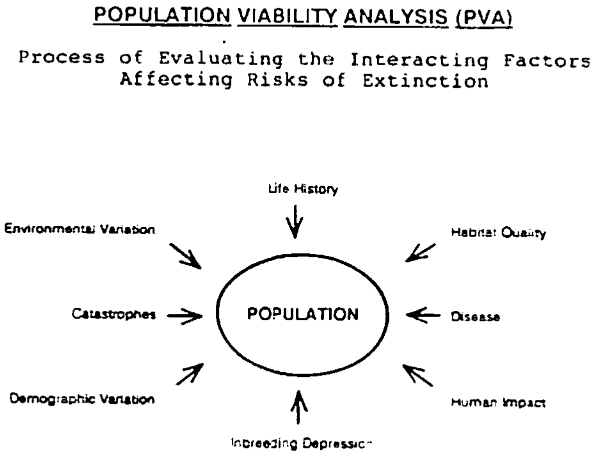

Figure 5. Population Viability Analyses (PVA) model the effects of different life-history, environmental and threat factors on the extinction and retention of genetic diversity in single populations.

measuring the level of genetic variation that is retained over time and recording if and when the population goes extinct (population size goes to zero). The simulations are repeated, often thousands of times, to provide estimates of the statistical variation associated with the results. The probability of extinction at any given time is measured as the number of simulations that the population had gone extinct by that time divided by the total number of simulations run (Figure 6). The levels of genetic variation are recorded as the percent of the original heterozygosity and number of original alleles retained in the population at any particular point.

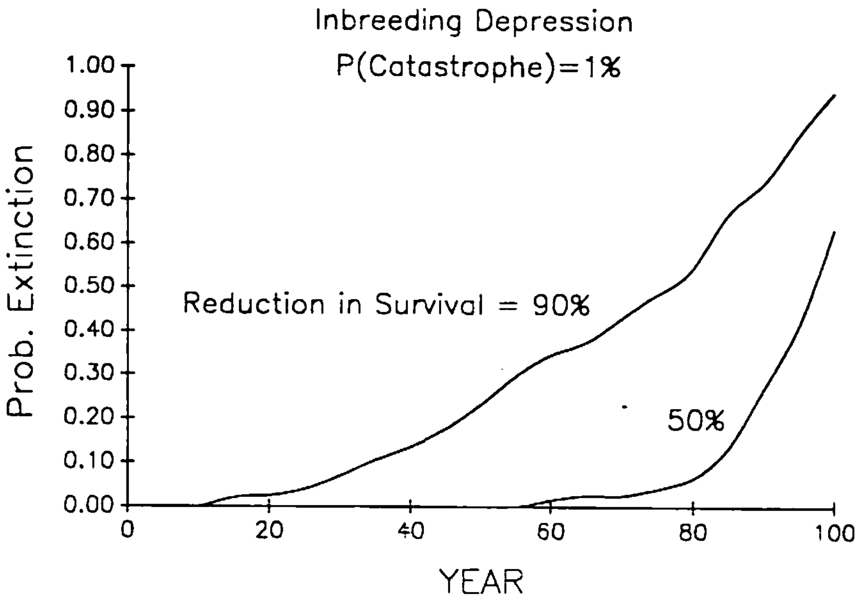

Figure 6. Hypothetical example of population extinction results from the VORTEX PVA model. The model includes negative effects of inbreeding and a catastrophe probability of 1%. The probability of extinction is shown over time for two different levels of catastrophe severity: a 90% reduction in survival vs 50% reduction in survival.

A number of population viability models have been developed. The model used by the Captive Breeding Specialist Group of the IUCN is VORTEX, written by Robert Lacy (Chicago Zoological Society). This model has been used extensively to develop conservation strategies for a number of species including the Black-footed ferret, Florida panther, Puerto Rican Parrot, Javan rhino and the four species of lion tamarins.

The true value of the model is not in trying to examine the effects of all variables simultaneously in the population. The interactions between these many factors is too complex to attempt to interpret the results of population projections based on more than just of few of these considerations. We can gain far more insight into the dynamics of the population by examining only one or two factors at a time - and picking those factors that we believe have an impact on the population and ignoring those that don't.

The primary use of the model in developing conservation strategies is its use in conducting "what if" analyses. For example 'what if' survival were decreased in the wild population as a result of a disease outbreak? How would that effect the extinction of the population and retention of genetic diversity? These 'what if' analyses can also be used to evaluate management recommendations. For example, how would the probability of population extinction change if the carrying capacity of the reserve holding the animals were increased by 10%?

Because the models don't examine all factors potentially contributing to extinction, the model results usually underestimate a population's probability of extinction. However, it is important to stress that the purpose of the PVA is not to estimate exact extinction probabilities but to identify the relative importance of the various factors being considered and to evaluate the effect of a range of management recommendations on the survival of the population.

IMPLICATIONS OF PVA ON MANAGEMENT GOALS

The concepts of population extinction and loss of genetic diversity are based on probabilities rather than certainties. The results from the PVA models provide us with information on the probability of extinction given certain assumptions about the biology and status of the population. As a result, we can not predict or guarantee what will happen to these populations with any absolute certainty.

This has some fairly strong implications when we are trying to develop conservation strategies to reduce the risks of extinction in the populations. We must be able to recognize that we will not be able to formulate and implement recommendations that will guarantee the survival of any population. We can only formulate and implement recommendations that will decrease the likelihood of extinction in populations over a given time period.

A common approach is to develop management strategies that assure a 95% chance of the population surviving for 100 years and maintaining 90% of its genetic variation over the same time period (Shaffer 1987; Soule et al, 1986). This would assure a high probability of survival and retain a large proportion of the population's ability to genetically adapt and evolve to changing environments. This approach defines the Minimum Viable Population (MVP) size to achieve these management objectives. Management strategies can only be fully evaluated if both degree of certainty and time frame for management are specified.

METAPOPULATIONS

The discussion to this point has focused on the extinction and genetic dynamics of a single population. However, often managers are faced with a species distributed over several interacting populations. When this is the case and animal movement (migration) between populations is high enough that the dynamics (extinction or genetic) of any single population is affected by dynamics of other nearby populations, the group of interacting populations is called a Metapopulation (Figure 7). The understanding of metapopulation dynamics has become increasingly important for the development of conservation strategies.

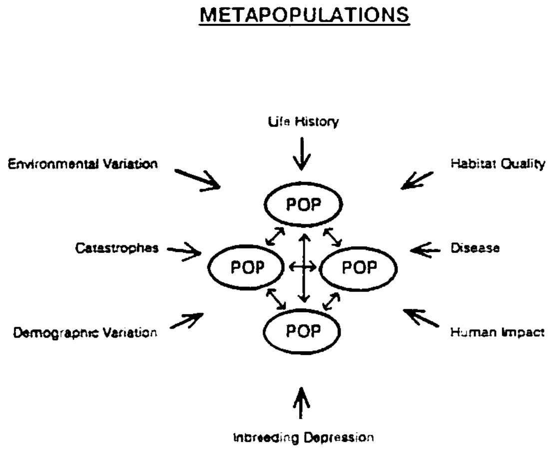

Figure 7. The interaction between population 'patches' results in a Metapopulation structure. Conservation strategies must consider the spatial distribution of the patches and its effect on correlated extinctions and recolonization between patches.

Metapopulation management focuses on the spatial distribution of the populations and how that influences both the genetic and demographic dynamics of the system. The metapopulation system can be thought of as a grouping of populations ('patches') of different sizes and distances from each other, with some patches periodically going extinct and being recolonized by migrants from other patches. The most important conservation considerations are rates of extinction for the individual patches and the re-colonization rates between patches (Gilpin 1987).

As we have discussed above, the extinction dynamics of any single patch is affected by any number of factors including size of population, rate of population recovery following a population decline, etc. From a metapopulation perspective, the simplest level is when patch extinction rates are uncorrelated with each other: the probability of extinction of any one patch is independent of any other patch. Environmental variation and catastrophes increase the extinction correlation between patches and this increases the likelihood of the entire metapopulation going extinct. So considerations of the spatial distribution between patches, and what that means in terms of how similarly they react to environmental variation and catastrophes is an important part of developing management strategies.

On the other side of the coin is the effect of spatial distribution on recolonization rates between patches. The closer patches are to each other, the higher the probability of a patch being recolonized following an extinction by migrants from a neighboring patch. Thus, distances between patches is positively correlated with recolonization and long-term survival of the metapopulation.

Patch extinction and recolonization also effect the retention of genetic diversity in the metapopulation. Small, fragmented and isolated populations rapidly lose genetic diversity. However, with migration between patches, gene flow among patches can be increased and the effective size of the total metapopulation is significantly increased. However, if recolonization following extinction repeatedly involves a very limited number of individuals (one pair or a pregnant female), then individual patches can be genetically invariant as a result of the recurrent founder effects.

The interaction between the positive aspects of recolonization and the negative effects of correlated patch extinction complicate the understanding of metapopulation dynamics, both at the genetic and demographic level. Unfortunately, computer models that combine aspects of single-population extinction and genetic considerations discussed above with considerations of metapopulation theory are not yet available for developing conservation management strategies.

Nevertheless, managers should be cognizant of the complexities of metapopulation systems. In general, populations distributed over several populations are more secure over the long-term than one population located at a single site. This is particularly true if there is gene flow between patches (either natural or through management intervention) and the patches are not susceptible to the same catastrophic threats. In many cases, a captive population can serve as a secure patch that can be used as a source to recolonize other patches through reintroduction efforts and as a reservoir for genetic diversity.

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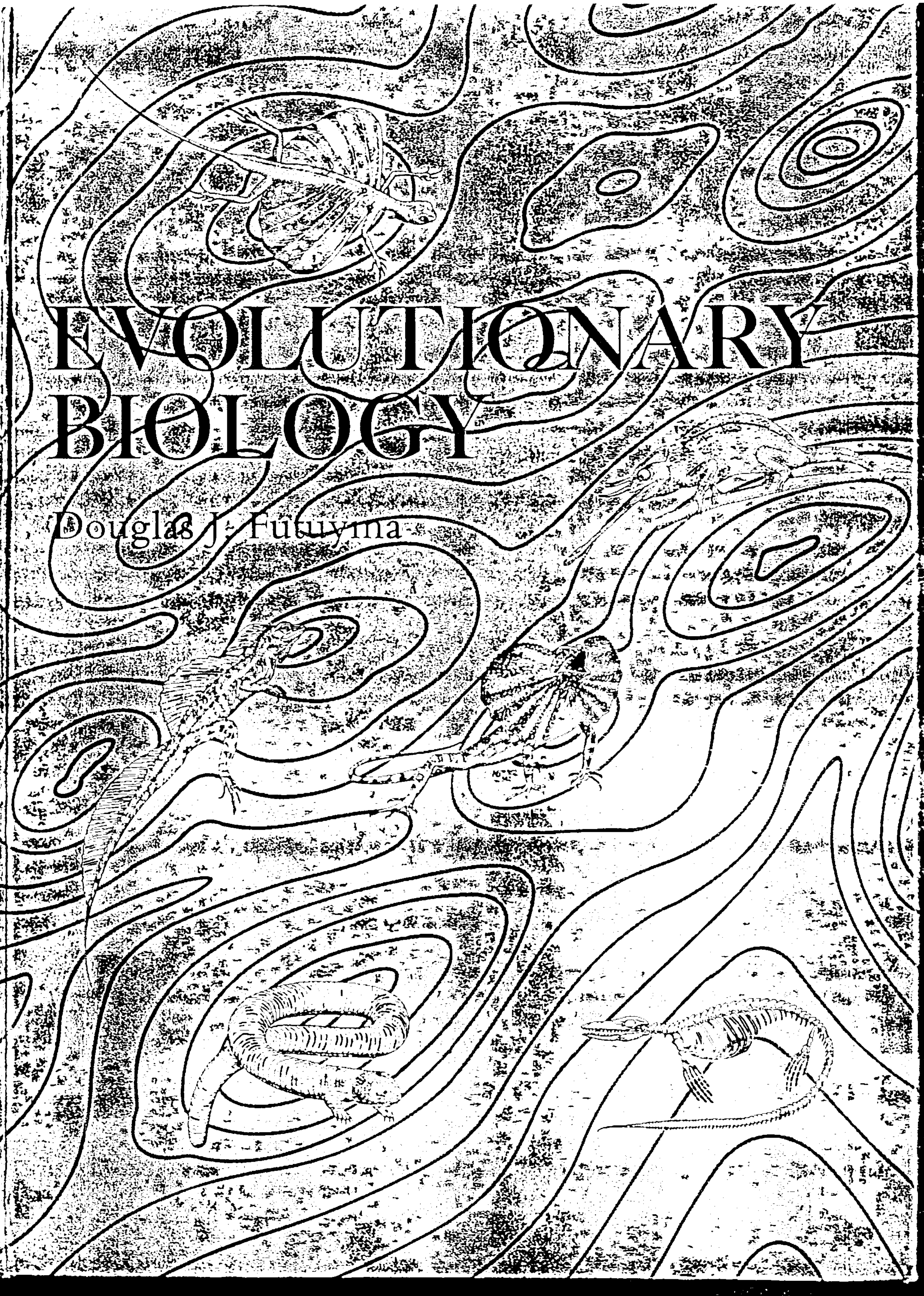
EVOLUTIONARY BIOLOGY

Douglas J. Futuyma



Total = Within ~ (1 − Within) [illegible]

B The Wahlund Effect: Genotype Frequencies in a Subdivided Population

Suppose a "population" consists of k subpopulations, each with a different gene frequency p_i. Among the subpopulations the mean gene frequency is $\bar{p} = \Sigma_i p_i/k$, and the variance in gene frequency is $V_p = \Sigma_i(p_i - \bar{p})^2/k$. Now note that V_p is

$$\frac{\Sigma_i(p_i^2 - 2p_i\bar{p} + \bar{p}^2)}{k} \text{ or } \frac{\Sigma_i p_i^2 - 2\bar{p}\Sigma_i p_i + \bar{p}^2}{k}.$$

But $\Sigma\, p_i = k\bar{p}$, so $V_p = \Sigma_i p_i^2/k - \bar{p}^2$. Thus $\Sigma_i p_i^2/k = \bar{p}^2 + V_p$. But $\Sigma_i p_i^2/k$ is the average proportion of AA homozygotes among the subpopulations, the proportion of AA in the population as a whole. Thus the frequency of this homozygous class exceeds the Hardy-Weinberg frequency ($\bar{p}^2$) by an amount V_p. Similarly the frequency of $A'A'$ in the entire population is $\bar{q}^2 + V_p$, and the frequency of heterozygotes is, by subtraction, $2\bar{p}\bar{q} - 2V_p$. This disparity between observed frequencies and Hardy-Weinberg frequencies is termed the Wahlund effect.

This result implies that an investigator who samples from what appears to be a single panmictic population, but is actually an aggregate of subpopulations that vary in gene frequency, will find an unexpected deficiency of heterozygotes. The magnitude of this deficiency is indeed a measure of the degree to which the "population" is actually structured into subpopulations (or, a measure of the variance in gene frequency among the subpopulations). Another such measure, of course, is F: the frequency of heterozygotes may be written either $2\bar{p}\bar{q} - 2V_p$ or $2\bar{p}\bar{q}(1 - F)$. Equating these, we find that $2(\bar{p}\bar{q} - V_p) = 2(\bar{p}\bar{q} - \bar{p}\bar{q}F)$, or $F = V_p/\bar{p}\bar{q}$.

This F, denoted F_{ST}, is different from the F that represents the average inbreeding coefficient of individuals derived from consanguineous matings within a subpopulation. It is useful to recognize, as Wright (1965) does, several levels of F:

- F_{IS} the probability that two gametes taken at random within an average subpopulation yield an autozygous individual
- F_{ST} the probability that two gametes taken at random from two different subpopulations yield an autozygote
- F_{IT} the probability that two gametes taken at random from the entire "population" yield an autozygote

Wright shows that the relationship among these can be written $F_{ST} = (F_{IT} - F_{IS})/(1 - F_{IS})$.

$1 - F_T$ [illegible]

THE EFFECT OF GENE FLOW

Probably few populations are completely isolated. The greater the amount of gene exchange among populations, the more similar their genetic composition will be, unless other factors counteract migration's homogenizing influence.

One such factor is natural selection, which maintains a permanent disparity in the gene frequencies of different populations if different alleles are favored in the various populations (*Box C*). This is reflected in many patterns of adaptive geographic variation. But if migration is strong enough, it can counteract selection to at least some extent, preventing a population from becoming fully adapted to its environment. For example, adult water snakes (*Natrix sipedon*) on the Lake Erie Islands are uniformly grayish in color, whereas mainland adults are strongly banded (*Figure 12*). Among young island snakes, however,

$(F_{ST})(1 - F_{IS}) = F_{IT} - F_{IS}$

$-F_{IT} = -(F_{ST})(1 - F_{IS}) - F_{IS}$

$1 - F$ [illegible]

The Population Viability Assessment Workshop: A Tool For Threatened Species Management

by

Tim W. Clark, Gary N. Backhouse, and Robert C. Lacy

Introduction

Population viability assessment (PVA) is a procedure that allows managers to simulate, using computer models, extinction processes that act on small populations and therefore assess their long-term viability. In both real and simulated populations, a number of interacting demographic, genetic, environmental, and catastrophic processes determine the vulnerability of a population to extinction. These four types of extinction processes can be simulated in computer models and the effects of both deterministic and stochastic forces can be explored. In turn, the outcome of various management options, such as reducing mortality, supplementing the population, and increasing carrying capacity can also be simulated. Thus, PVA provides managers with a powerful tool to aid in assessing the viability of small populations and in setting target numbers for species recovery as a basis for planning and carrying out recovery programs. In addition, having performance-based management programs enables progress to be quantified and assessed. PVA also offers managers a powerful strategic planning and policy tool when vying for limited financial resources. This paper describes a PVA workshop that used a stochastic computer simulation to model small populations of, and explore management options for, six threatened/endangered wildlife species in Victoria, Australia.

The Workshop

The workshop was co-sponsored by the Department of Conservation and Environment (DCE), Victoria, and the Zoological Board of Victoria (ZBV), in cooperation with the Chicago Zoological Society (CZS) and was held at the Arthur Rylah Institute for Environmental Research (DCE), Heidelberg, Victoria, from May 28 through June 1, 1990.

The objectives of the workshop were to: 1) examine the adequacy of data on the six threatened species; 2) simulate the vulnerability to extinction by using PVA; 3) examine outcomes of various management options to restore the species; 4) estimate population targets needed for recovery planning; 5) evaluate the potential of PVA as a teaching aid to illustrate extinction processes and management options.

Mountain pygmy-possum Photo by Ian McPherson

The six species were: mountain pygmy-possum, *Burramys parvus*; leadbeater's possum, *Gymnobelideus leadbeateri*; eastern barred bandicoot, *Perameles gunnii*; long-footed potoroo, *Potorous longipes*; orange-bellied parrot, *Neophema chrysogaster*, and helmeted honeyeater, *Lichenostomus melanops cassidix*.

The 32 people attending the workshop represented experienced field biologists and wildlife managers with detailed knowledge of these and other threatened species. A month prior to the workshop all participants were provided with background reading material (e.g. Shaffer 1981, Brussard 1985, Samson 1985, Gilpin 1989, and Lacy and Clark 1990). A questionnaire on life-history parameters to be completed on each species as a basis for entering values into the computer was also provided. Following an introduction and overview of PVA, the participants formed teams and commenced work. Simulations, analyses, and discussions were ongoing over the next five days. The first week concluded with a report and review of each team's progress. During the following week, teams further refined their simulations and commenced preparation of a final report with management recommendations.

Population Viability Analysis: The Vortex Model

The workshop used a computer program, VORTEX, to simulate demographic and genetic events in the history of a small population (<500 individuals). VORTEX was written in the C programming language by Robert Lacy for use on MS-DOS microcomputers. Many of the algorithms in VORTEX were taken from a simulation program, SPGPC, written in BASIC by James Grier (Grier 1980a, 1980b, Grier and Barclay 1988). See Lacy et al. 1989, Seal and Lacy 1989 and Lacy and Clark 1990 for earlier uses of VORTEX.

Life table analyses yield average long-term projections of population growth (or decline), but do not reveal the fluctuations in population size that would result from variability in demographic processes. When a population is small and isolated from other populations of conspecifics, these random fluctuations can lead to extinction, even in populations that have positive population growth on average. Fluctuations in population size can result from several levels of stochastic effects. Demographic variation results from the probabilistic nature of birth and death processes. Therefore, even if the probability of an animal reproducing or dying is always constant, the actual number reproducing or dying within any time interval would vary according to the binomial distribution with mean equal to the probability of the event (p), and variance given by $Vp = p^*(1-p)/N$. Demographic variation is thus intrinsic to the population and occurs in the simulation because birth and death events are determined by a random process (with appropriate probabilities). Environmental variation (EV) is the variation in the probabilities of reproduction and mortality that occur because of changes in the environment on an annual basis (or other timescales).

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, whether each adult female produces broods of size 0, 1, 2, 3, 4, or 5 during each year, and which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Mortality and reproduction probabilities are sex-specific. Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. Fecundity is assumed to be independent of age after an animal reaches reproductive age. The mating system can be specified to be either monogamous or polygynous. In either case, the user can specify that only a subset of the adult male population is in the breeding pool (the remainder being excluded perhaps by social factors). Those males in the breeding pool all have equal probability of siring offspring.

Each simulation is started with a specified number of males and females in each pre-reproductive age class and the breeding age class. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus. The user specifies the severity of inbreeding depression which is expressed in the model as a loss of viability in inbred animals. The computer program simulates and tracks the fate of each population and then produces summary statistics on: the probability of population extinction over specified time intervals; the mean time to extinction of those simulated populations that went extinct; the mean size of populations not yet extinct; and the levels of genetic variation remaining in any extant populations.

A population carrying capacity specified by the user is imposed by a probabilistic truncation of each age class if, after breeding, the population size exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity, as linear increases or decreases across a specified number of years.

VORTEX models environmental variation simplistically (which is both an advantage and disadvantage of simulation modelling), by selecting at the beginning of each year the population age-specific birth rates, age-specific death rates, and carrying capacity from distributions with means equal to the overall averages specified by the user, and with variances also specified by the user. Unfortunately, rarely do we have sufficient field data to estimate the fluctuations in birth and death rates, and in carrying capacity, for a wild population. The population would have to be monitored long enough to separate sampling error statistically from demographic variation in the number of births and deaths, from annual variation in the probabilities of these events. Such variation can be very important in determining the probability of extinction, yet we rarely have reasonable estimates for most populations of conservation concern. If data on annual variation are lacking, a user can try various values, or model the fate of the population in the absence of any environmental variation.

Endangered Species
UPDATE

A forum for information exchange on endangered species issues
December 1990
Vol. 8 No. 2

Alice Clarke and Joel Heinen...Editors
Dr. Terry Root............Faculty Advisor
Jon Jensen.......................Staff Advisor

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Leadbeater's possum
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VORTEX can model catastrophes as events that occur with some specified probability and which reduce survival and reproduction for one year. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (i.e. a binomial process is simulated). If a catastrophe occurs, the probability of breeding is multiplied by a severity factor that is drawn from a binomial distribution with a mean equal to the severity specified by the user. Similarly, the probability of survival for each age class is estimated in a similar manner.

VORTEX also allows the user to supplement or harvest the population for any number of years in each simulation. The numbers of immigrants and removals are specified by age and sex. VORTEX outputs the observed rate of population growth (mean of N[t]/N[t-1]) separately for the years of supplementation/harvest and for the years without such management, and allows for reporting of extinction probabilities and population sizes at whatever time interval is desired (e.g. summary statistics can be given at 5-year intervals in a 100-year simulation).

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Because it is a detailed model of population dynamics, often it is not practical to examine all possible factors and all interactions that may affect a population. The user, therefore, must specify those parameters that can be estimated reasonably, leave out of the model those that are thought not to have a substantial impact on the population of interest, and explore a range of possible values for parameters that are potentially important but very imprecisely known. A companion program, VORPLOTS, was used at the workshop to produce plots of mean population size, time to extinction, and loss of gene diversity from simulation results.

Equipment Required

VORTEX requires an MS-DOS microcomputer with at least 640K of memory. A math co-processor speeds up the program substantially. The VORPLOTS plotting program produces files in the Hewlett Packard Graphics Language (HPGL), for use on an HP plotter or equivalent.

A Kodak Dataview EGA enabled projection of a computer display via an overhead projector onto a large screen so that all participants could observe demonstrations of VORTEX during initial training.

Computers were used during the daily sessions primarily for exploratory analyses with relatively few runs (100 or fewer) of a simulation; more extensive analyses were run overnight. A test with 100 runs would take from 15 minutes to 3 hours, depending on the machine used and the size of the population being simulated.

The Workshop Results

Each team documented its activities and provided a preliminary report of the simulations completed, conclusions, an assessment of the conduct of the workshop, and the usefulness of the PVA process. Results will be published in peer-reviewed scientific journals by each team.

All cases showed similar results. First, most species and populations were highly susceptible to local extinction. Any further habitat loss or fragmentation or reduction in population size and density would result in rapid extinction. Second, in all cases, more field data would have been helpful. Third, management options to stave off extinction were identified and results simulated. Options included strict habitat protection, enhancement of existing habitat or restoration of lost habitat, captive breeding, and reintroduction of animals to existing habitat patches in which the species has become extinct in recent decades or to newly created habitat. Various combinations of management strategies were recommended for future management. Fourth, the simulations demonstrated that if proactive conservation management had been undertaken even 5 to 10 years ago when populations and habitats were considerably larger, the task of present day managers would be much more tractable. And fifth, improved conservation management for all six species is expected to result from the PVA exercise, enhanced research, and subsequent on-the-ground management. Three cases illustrate these conclusions: the mountain pygmy-possum (Mansergh et al. in prep.), eastern barred bandicoot (Myroniuk and Patrick in prep.), and orange-bellied parrot (Brown et al. in prep.).

Mountain Pygmy-Possum: The mountain pygmy-possum is a small marsupial restricted to alpine and sub-alpine (>1500m altitude) rock screes and boulderfields with heathlands. The species has been well studied and much information is available on its ecology (Mansergh 1989). Diet consists of invertebrates, seeds, and fruits. Breeding occurs from September to December, with litter size of 3 to 4. The young become independent by mid-January. Females can breed in their first year, and can live up to 9 years. An unusual feature of the life history of *Burramys* is the fact that sexes are segregated during the non-breeding season. The adult population is heavily biased towards females (6F:1M) because of the very high mortality experienced by males post-dispersal.

The current total population is estimated to be 2,300 breeding adults of which 80% are females. The species is regarded as vulnerable in Victoria and rare in New South Wales. The species is also susceptible to climatic changes associated with global warming.

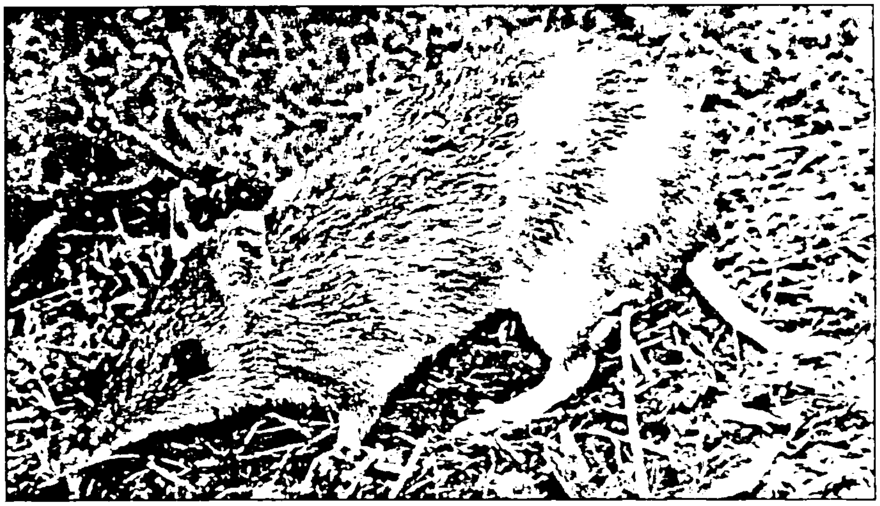
The mountain pygmy-possum exists as a number of discrete populations isolated from each other on mountain tops. A total of seven populations, ranging from 20-850 individuals (representing the situation in the wild) was modelled. High probabilities of extinction were observed in all small (<150 animals) populations at 25 and 50 years; this could account for the absence of the species from apparently suitable habitat within its range. The larger populations had a decreased likelihood of extinction. When modelled with a small but steady decrease in carrying capacity (1% per annum) such as could occur through climatic change with global warming, the probability of extinction increased greatly (to 45% in the case of the largest Victorian population of 850 individuals, over 50 years).

(Continued on UPDATE page 4)

Disturbance to habitat and further fragmentation of populations would increase the likelihood of extinction.

Eastern Barred Bandicoot: The mainland population of this marsupial species was formerly distributed over about 23,000 sq km of volcanic grassland in western Victoria. This population has now declined to 200 or fewer individuals restricted to remnant habitat near Hamilton (Clark and Seebeck 1990). The species is polygynous, with females capable of breeding from 3 months of age and males from 4 months of age. Gestation lasts about 12 days, with litters comprised of 1 to 5 offspring (usually 2-3); young remain in the pouch about 55 days. Females are capable of producing several broods per year. In spite of the very high reproductive potential, the population is believed to be declining at about 25% per annum. Juvenile mortality at dispersal from the nest is very high (> 90% within the first year). The decline of the species is attributed to habitat modification from pastoral activities and predation from introduced predators, including the red fox (*Vulpes vulpes*) and the cat (*Felis catus*).

Wild and captive populations of the eastern barred bandicoot were simulated. Modeling the wild population using available data without any change to current management indicated a 100% probability of extinction within 25 years, with a mean time to extinction of 7.2 years (± 2.1). Doubling the carrying capacity and leaving mortality unchanged had negligible impact on the probability of extinction and increased the mean time to extinction by only 2 years. Doubling the carrying capacity, reducing mortality by 30% and supplementing the wild population with the liberation of captive-bred animals greatly enhanced prospects for survival of the wild population. Under this scenario the probability of extinction was reduced to 0% over 25 years with a mean final population size of close to the carrying capacity of 300 animals. Modeling the existing and proposed captive populations allowed investigation of a variety of scenarios. The existing captive population of 16 pairs has an extinction probability of 83% over 25 years, with a mean time to extinction of 21.5 years. Doubling the number of adult pairs decreased the extinction probability to 0% but the surviving population had very low genetic variability, and there is little potential to harvest juveniles for release into the wild. Increasing the captive population to 62 adult pairs increased genetic variability and the potential to harvest juveniles without jeopardizing the captive population. Maintaining a captive population of 62 adult pairs (in two groups at separate locations to avoid catastrophe but managed as one population) and establishing two semi-captive populations with a capacity for 400 animals gave the best prospects for long term survival, maintenance of genetic variability, and production of sufficient offspring to consider reintroductions to suitable habitat within their former range. The exercise highlighted the need for a combination of management actions, rather than any single action, to prevent the almost certain extinction of the wild population under the existing management regime. Reduction of mortality by predator control and traffic management is essential for the survival of the eastern barred bandicoot. Captive management will be an important part of the recovery program, but with a more intensive program than that currently underway.



Eastern barred bandicoot

Photo by J. Seebeck

Orange-bellied Parrot: The biology and ecology of the orange-bellied parrot is comparatively well known (Loyn et al. 1986). The species is one of the rarest and most threatened birds in Australia, with a total population of 150-200 individuals. The orange-bellied parrot breeds in coastal southwest Tasmania in woodlands adjoining extensive sedgelands. After breeding, it migrates across Bass Strait to overwinter in coastal regions of southern mainland Australia. The birds feed in a variety of coastal habitats including grassland, saltmarsh, and dune systems, showing strong preferences for particular habitats and food types in different parts of their winter range and at different times of the year. An estimated 40 breeding pairs annually produce a total of 50-70 juveniles. The orange-bellied parrot is considered endangered. Loss of coastal habitat for development and trapping for the aviculture trade are considered to be the primary causes of the species' past decline. Pressures for development on or adjacent to its main wintering areas and habitat alteration are now the main threats to its survival. A captive breeding program is now underway as part of a range of measures undertaken to ensure the future survival of the species.

Populations were modelled using the current carrying capacity (150), a reduced carrying capacity (50), and an increased carrying capacity (500). Simulations which involved varying mortality, capture, and supplementation rates of the wild population were run for all carrying capacities. Simulating the existing population using current data and management regimes indicated that the species would remain extant over the next 50 years at least, and stood a good chance of surviving for 100 years.

Reducing the carrying capacity to 50 under current conditions somewhat surprisingly did not increase the probability of extinction over 50 years, although genetic variability was greatly diminished. As would be expected, increasing the carrying capacity to 500 birds further reduced the prospects of extinction and greatly increased the genetic variability of the population. When modelled with an increased juvenile mortality rate (75% cf 50%), the population with the reduced carrying capacity showed a 70% probability of extinction within 50 years, while the current and increased carrying capacity populations showed extinction probabilities of 20% within that time. Imposing a capture and release captive breeding program on the populations only slightly decreased the extinction probability of the reduced carrying capacity, high mortality population, but greatly improved heterozygosity in the reduced carrying capacity, current mortality population. No extinctions occurred in the current and increased carrying capacity populations even at the high mortality levels, when simulated with supplementation from a captive breeding program. The simulations indicate several points. Juvenile mortality is of great significance to the health of the population. Any increase above the present rate of 50% greatly increases the probability of extinction, even with an enhanced habitat carrying capacity. The captive breeding program is an important back-up to the wild population, and will be extremely valuable if the wild population declines.

Evaluation of the Workshop

An evaluation was considered to be an important part of the workshop. All participants rated the background material supplied prior to the workshop as good to very good. Provision of background material was essential as very few participants had any prior experience with PVA. Organization was rated as very good to excellent by participants. The key to success was the large number of microcomputers available so that 2 to 3 people per computer was possible. Presentations were rated as very good to excellent.

The workshop format was considered to be a highly successful way of presenting PVA. PVA was considered to be a useful tool to aid threatened species management, providing its application and limitations were understood. PVA can focus attention on questions that should be addressed through additional research. PVA can be applied to well-studied taxa, and the general principles can be applied more widely to other taxa providing program characteristics are kept in perspective. All participants would recommend PVA as a management tool.

Conclusions

The PVA workshop proved a very useful way of quickly learning a new technique for threatened species management and conservation. PVA was applied to six species allowing a critical, quantitative analysis of extinction probabilities, as well as exploring management options to prevent species loss. PVA results will be used in forthcoming management plans and actions directed towards restoring these species to a status from which they will be relatively immune to extinction from random processes. In the future, it can be expected that PVA's will be carried out on additional endangered species to help manage their recovery.

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Author affiliations are as follows: T. Clark. Department of Conservation Biology, Chicago Zoological Society, Brookfield, IL, 60513, USA and School of Forestry and Environmental Studies, Yale University, New Haven, CN, 06511, USA; G. Backhouse. Wildlife Management Branch, Department of Conservation and Environment, PO Box 137, Heidelberg, Victoria, 3084, Australia.; R. Lacy. Department of Conservation Biology, Chicago Zoological Society, Brookfield, IL, 60513, USA.

Estimates of Lethal Equivalents and the Cost of Inbreeding in Mammals

KATHERINE RALLS
Department of Zoological Research
National Zoological Park
Smithsonian Institution
Washington, D.C. 20008, U.S.A.

JONATHAN D. BALLOU
Department of Zoological Research
National Zoological Park
Smithsonian Institution
Washington, D.C. 20008, U.S.A.

ALAN TEMPLETON
Department of Biology
Washington University
St. Louis, Missouri 63130, U.S.A.

Abstract: *The costs of inbreeding in natural populations of mammals are unknown despite their theoretical importance in genetic and sociobiological models and practical applications in conservation biology. A major cost of inbreeding is the reduced survival of inbred young. We estimate this cost from the regression of juvenile survival on the inbreeding coefficient using pedigrees of 40 captive mammalian populations belonging to 38 species.*

The number of lethal equivalents ranged from − 1.4 to 30.3, with a mean of 4.6 and a median of 3.1. There was no significant difference between populations founded with wild-caught individuals, a mixture of wild-caught and captive-born individuals, and individuals of unknown origin. The average cost of a parent-offspring or full sibling mating was 0.33, that is, mortality was 33% higher in offspring of such matings than in offspring of unrelated parents. This is likely to be an underestimate.

Resumen: *Los costos de procreación en consanguinidad en poblaciones naturales de mamíferos son desconocidos a pesar de su importancia teórica en los modelos genéticos y sociobiológicos y en sus aplicaciones prácticas para la biología de la conservación. Uno de los costos mayores de la procreación en consanguinidad es la disminución en la sobrevivencia de las crías consanguíneas. Estimamos este costo por medio de la regresión de la sobrevivencia juvenil en el coeficiente de procreación en consanguinidad utilizando pedigrís de 40 poblaciones de mamíferos en cautiverio pertenecientes a 38 especies.*

El número de equivalentes letales varió de − 1.4 a 30.3, con una media de 4.6 y una mediana de 3.1. No hubo diferencia significativa entre poblaciones formadas a partir de individuos silvestres capturados, a partir de una mezcla de individuos silvestres capturados, y a partir de individuos de origen desconocido. El costo promedio del apareamiento de padre-cría o hermanos completamente consanguíneos fue de 0.33, es decir, la mortalidad fue 33% más alta en las crías de tales apareamientos que en las crías de especies no relacionadas. Es probable que este cálculo sea una subestimación.

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Introduction

Many studies of laboratory, domestic, and zoo animals have documented reduced survival and fecundity of inbred young (Wright 1977; Ralls & Ballou 1983; Sausman 1984; Templeton & Read 1984). Inbreeding depression is thus a major concern in the management of small populations, and estimates of the cost of inbreeding are of considerable importance to conservation biology.

However, inbreeding can increase an individual's inclusive fitness by producing young that share more of its genome. Thus, when inbreeding has little or no genetic cost, there should be strong selective advantage for inbreeding as well as recognition and cooperation among kin (Wilson 1976; May 1979). The cost of inbreeding is therefore of theoretical importance as well.

Calculations of the total cost of inbreeding in natural populations would involve considering the effects of inbreeding on several components of fitness. However, the "cost of inbreeding" that appears in a variety of theoretical models (Dawkins 1976; Bengtsson 1978; Parker 1979; Smith 1979; Feldman & Christiansen 1984) is defined solely in terms of the survival of inbred young relative to non-inbred young. There are almost no estimates of this quantity in natural populations of mammals (Packer 1979).

We estimate this cost from pedigrees of 40 captive mammalian populations belonging to 38 species.

Methods

Morton, Crow, & Muller (1955) developed a log model for estimating the cost of inbreeding from the rate at which juvenile survival decreases with increasing amounts of inbreeding. Specifically,

$$S = e^{-(A + BF)} \qquad (1)$$

where S is the proportion of individuals surviving to some age, F is the inbreeding coefficient, A is considered a measure of death due to environmental causes and the genetic damage expressed in a randomly mating population, and B is a measure of the rate at which survival decreases with increasing inbreeding.

Makov & Bittles (1986) evaluated the use of this and several other equations to estimate effects of inbreeding in humans. They found that many different models could adequately detect significant inbreeding effects; however, different models resulted in different values of A and B. Because of the limited range of inbreeding levels in available data from human populations (F = 0–0.125), they were unable to determine which equation most adequately modeled data on inbreeding effects in humans. They suggested that different equations could more effectively be evaluated in animal populations with wider ranges of inbreeding levels.

We evaluated the log transformed equation (1) and two other equations, using several of our largest data sets with relatively wide ranges of inbreeding levels (F = 0–0.5). The two additional equations were

$$S = A + B(F) \qquad (2)$$

$$\arcsin\sqrt{S} = A + B(F) \qquad (3)$$

where S, A, B, and F are the same values as in equation (1). Model 2 was used because it represents the simplest linear relationship between the variables. Model 3 (angular transformation) was used since it is often recommended for estimating proportions (Sokal & Rohlf 1969). Weighted least squares regression, with a small sample size correction (Templeton & Read 1984), was used to estimate the parameters for each of the models. The total percentage of variation explained by the equation (R^2) was used to evaluate which model best fitted the data.

When analyzing pedigrees of zoo animals, care must be taken to distinguish inbreeding depression from hybridity effects or "outbreeding depression" (Templeton & Read 1984; Templeton et al. 1986). We therefore carried out the analysis developed for this purpose by Templeton & Read (1984) on those pedigrees with adequate sample sizes but found no evidence of outbreeding depression (Templeton & Read 1984; unpublished data).

Inbreeding coefficients (F) were calculated for each animal in each pedigree, relative to the founders of the population. Methods for calculating F from pedigree data are given by Ballou (1983). F is the probability that the two alleles present at a given locus are "identical by descent"—that is, are derived by replication of a single allele from a common ancestor. F ranges from 0 in a non-inbred individual to 1.0 in a completely inbred (homozygous) individual (Crow & Kimura 1970). The effect of inbreeding is often less severe in individuals with inbred ancestors (Bowman & Falconer 1960; Lorenc 1980; Templeton & Read 1984), but we were unable to exclude them from the analysis because this eliminated all levels of inbreeding except F = 0.25 in many pedigrees.

Levels of inbreeding varied among pedigrees (Table 1). For each level of inbreeding represented in a particular pedigree, we calculated the proportion of animals that survived to a criterion age. This was 180 days for the larger species and one-half the age at sexual maturity for the smaller ones (Table 2). Ideally, studies of the relationship between inbreeding and juvenile mortality should be based upon the total mortality before reaching reproductive age (Cavalli-Sforza & Bodmer 1971), but we were unable to follow many individuals for this period because zoo animals are often transferred to other institutions before reaching reproductive age. Considering survival to a criterion age less than repro-

Table 1. Comparison of models used for estimating cost of inbreeding.

SPECIES[a]	*Maximum Inbreeding level*	*Comparison of R^2 Values MODEL* Log (1)	Linear (2)	Arcsin (3)
Short bare-tailed opossum	.328	.80	.79	.77
Elephant shrew	.125	.05	.06	.07
Golden lion tamarin	.375	.35	.26	.26
Greater galago	.250	.17	.14	.13
Maned wolf	.312	.77	.83	.83
Bush dog	.500	.02	.00	.00
Pygmy hippopotamus	.375	.45	.55	.55
Dorcas gazelle	.375	.64	.66	.63

[a] *Scientific names listed in Table 2.*

ductive maturity tends to underestimate the cost of inbreeding, as inbred mortality increases more rapidly than non-inbred mortality with increasing age in some species (Ralls, Brugger, & Glick 1980; unpublished data).

Results

Table 1 shows the results of the three models applied to eight of the largest data sets. R^2 values were highest for the Linear model (2) in 2 populations, highest for the Arcsin model (3) in 2 populations, and highest for the log model (1) in 4 populations. As Makov and Bittles (1986) concluded, no one model was clearly better than the others; R^2 values ranged over only a few percentage points across the models.

The log transformed model (1) has been used extensively in the literature to estimate number of lethal equivalents and is the theoretically expected model, if it is assumed that genetic and environmental influences are independent of each other with respect to survival (Morton, Crow & Muller 1955). Use of this model also facilitates comparisons with A and B values already published in the literature. We therefore selected it for all subsequent analyses.

Estimates for A and B are shown in Table 2. Values of A ranged from 0.03 to 1.11 with a mean of 0.33 and a median of 0.32. Values for B ranged from −0.68 to +15.16, with a mean of +2.33 and a median of +1.57 (Fig. 1). Of the 40 populations, 36 had positive slopes, which clearly indicates an overall trend towards higher levels of juvenile mortality with increasing inbreeding coefficients (Sign test, $P < .001$). This relationship was statistically significant—that is, the slope of the line was significantly greater than zero—in only 9 (23%) of the populations. However, most of our sample sizes were small and distributed over only a few levels of inbreeding. The statistical power to detect slopes significantly greater than zero was therefore limited. Considering only those populations in which the relationship between inbreeding and survival is significant would be likely to greatly overestimate the average cost of inbreeding in mammals. Limiting the analysis to only those species with relatively large data sets increases the power of the statistical comparisons but reduces the number of species that can be analyzed. Only 10 species had more than five levels of inbreeding and total sample sizes over 100. Six of these 10 had slopes significantly different from zero; the average B value was 1.98, with a median of 1.64. These B values did not differ significantly from those in the overall data set (Mann-Whitney U test, $P > 0.05$).

The distributions of B by order are shown in Figure 2. Median values were between one and two except for the Carnivora. There were no statistically significant differences between average B values in populations founded with wild-caught individuals ($\bar{x} = 2.57$, $n = 18$), a mixture of wild-caught and captive individuals ($\bar{x} = 2.42$, $n = 11$), and individuals of unknown origin ($\bar{x} = 1.95$, $n = 10$) (Kruskal-Wallis Test, $P = 0.88$).

The number of lethal equivalents per gamete lies between B and A but is usually very close to B (Cavalli-Sforza & Bodmer 1971; Crow & Kimura 1970). The number per zygote or individual is twice the number per gamete, thus our estimates of the average number of lethal equivalents per individual are twice the values of B in Table 2, with a mean of 4.6 and a median of 3.1. We estimated the cost of inbreeding for matings between first-degree relatives (parents and their offspring or full siblings) by solving equation (1) for each species using F = 0 and F = 0.25 to obtain the predicted survivorship at these levels of inbreeding. The cost of inbreeding (i) at F = 0.25 is then equal to

$$i = 1 - \left[\frac{\text{Survivorship at } F = 0.25\text{: } e^{-(A+.25B)}}{\text{Survivorship at } F = 0\text{: } e^{-(A)}}\right]$$

$$= 1 - e^{-.25B} \qquad (4)$$

The average cost of inbreeding between first degree relatives, calculated by averaging the costs across all populations, was 0.33 (Table 2). Solving equation (4)

Table 2. The cost of inbreeding in 40 mammalian populations.

TAXON	Survival to Age (Days)	N	Founder^{a} Type	No. of Inbred Levels	Model Estimates A	Model Estimates B	Model R^2	Cost of Inbreeding^{c} at $F = 0.25$	Data Source
MARSUPIALIA									
Short bare-tailed opossum (*Monodelphis domestica*)	75	251	W	6	0.03	0.43^{b}	0.80	10	National Zoo
Parma wallaby (*Macropus parma*)	180	17	W	5	0.32	1.69	0.47	34	National Zoo
INSECTIVORA									
Elephant shrew (*Elephantulus rufescens*)	21	218	W	7	0.28	2.12	0.05	41	National Zoo
PRIMATES									
Black spider monkey (*Ateles fusciceps robustrus*)	180	23	W	3	0.23	2.22	0.88	.43	National Zoo
Saddle-backed tamarin (*Saguinus fuscicollis*)	180	233	U	2	1.11	1.86	—	37	Monell Chemical Senses Center
Illiger's saddle-backed tamarin (*Saguinus f. illigeri*)	180	406	U	4	0.40	7.92	0.40	.82	Rush-Presbyterian St. Luke's Medical Center
Golden lion tamarin (*Leontopithecus r. rosalia*)	180	974	W	18	0.54	2.15^{b}	0.35	42	1984 Studbook
Ring-tail lemur (*Lemur catta*)	180	53	M	4	0.34	0.13	0.01	03	Oregon Primate Research Center
Black lemur (*Lemur macaco*)	180	43	W	3	0.52	2.78	0.87	50	Oregon Primate Research Center
Brown lemur (*Lemur fulvus*)	180	136	M	6	0.32	9.17^{b}	0.94	90	Oregon Primate Research Center
Greater galago (*Galago c. crassicaudatus*)	180	251	M	29	0.45	1.69^{b}	0.17	34	Oregon Primate Research Center
Melanotic galago (*Galago c. argentatus*)	180	54	M	4	0.36	0.48	0.19	.11	Oregon Primate Research Center
Crab-eating macaque (*Macaca fascicularis*)	180	237	U	3	0.37	0.29	0.56	.07	New England Primate Research Center
Celebes black ape (*Macaca nigra*)	180	86	U	3	0.38	2.84	0.70	.51	Oregon Primate Research Center
Chimpanzee (*Pan troglodytes*)	180	247	U	4	0.35	1.05	0.67	23	Yerkes Primate Center
RODENTIA									
Climbing rat (*Tylomys nudicaudus*)	45	49	U	5	0.23	0.14	0.02	- 04	National Zoo
Wied's red-nosed rat (*Wiedomys pyrrhorhinos*)	30	23	W	2	0.05	15.16	—	98	National Zoo
Rock cavy (*Kerodon rupestris*)	90	132	U	3	0.12	0.77	0.87	18	National Zoo
Salt-desert cavy (*Dolichotis salinicola*)	90	17	W	2	0.08	7.21	—	34	National Zoo
Acouchi (*Myoprocta pratti*)	135	36	U	5	0.30	2.20	0.17	42	National Zoo
Boris (*Octodontomys gliroides*)	75	53	U	6	0.26	1.15	0.33	25	National Zoo
Punare (*Cercomys cunicularus*)	60	161	W	4	0.10	0.94^{b}	0.91	21	National Zoo
CARNIVORA									
Maned wolf (*Chrysocyon brachyurus*)	180	338	M	4	0.52	-0.68	0.77	- 19	1983 Studbook
Bush dog (*Speothos venaticus*)	180	176	W	9	0.54	0.24	0.02	.06	1983 Studbook
Sumatran tiger (*Panthera tigris sumatrae*)	180	427	M	12	0.49	0.01	0.00	003	1983 Studbook
PERISSODACTYLA									
Zebra (*Equus burchelli*)	180	50	U	2	0.30	1.56	—	32	National Zoo
ARTIODACTYLA									
Pygmy hippopotamas (*Choeropsis liberiensis*)	180	419	W	12	0.33	1.59^{b}	0.45	.33	1982 Studbook

Table 2. Continued

TAXON	Survival to Age (Days)	N	Founder Type[a]	No. of Inbred Levels	Model Estimates		Model R^2	Cost of Inbreeding[c] at F = 0.25	Data Source
					A	B			
Reeves muntjac (*Muntiacus reevesi*)	180	75	M	9	0.19	1.20	0.37	26	National Zoo
Eld's Deer (*Cervus eldi thamin*)	180	24	M	2	0.31	7.57	—	.85	National Zoo
Pere David's Deer (*Elaphurus davidianus*)	180	39	C	7	0.17	0.63[b]	0.74	15	National Zoo
Reindeer (*Rangifer tarandus*)	180	50	W	4	0.32	4.20	0.71	.65	National Zoo
Giraffe (*Giraffa camelopardalis*)	180	19	W	2	0.29	2.24	—	.43	National Zoo
Kudu (*Tragelaphus strepsiceros*)	180	25	W	2	0.37	−0.03	—	−.01	National Zoo
Bongo (*Tragelaphus eurycerus*)	180	74	W	3	0.23	−0.55	0.74	−.15	1984 Studbook
Gaur (*Bos gaurus*)	180	182	W	6	0.18	0.51	0.36	.12	Hinz & Foose, 1982
Scimitar-horned oryx (*Oryx dammah*)	180	81	M	2	0.09	4.63	—	.69	National Zoo
Wildebeest (*Connochaetes taurinus*)	180	42	W	11	0.33	0.28	0.02	.07	National Zoo
Dik-dik (*Madoqua kirki*)	180	20	M	3	0.80	0.59	0.12	.14	National Zoo
Dorcas gazelle (*Gazella dorcas*)	180	143	M	15	0.34	1.85[b]	0.64	37	National Zoo
Spekes gazelle (*Gazella spekei*)	30	64	W	5	0.22	3.08[b]	0.92	54	Templeton & Read, 1983
		Mean:			0.33	2.33		0.33	
		Median:			0.32	1.57		0.33	
		Lower Quartile:			0.23	0.45		0.09	
		Upper Quartile:			0.39	2.81		0.47	

[a] Founder Type: W = All founders wild-caught.
C = Founders captive-born.
M = Founders were a mix of wild-caught and captive-born.
U = Source of founders unknown.

[b] B (slope) significantly different than zero at the 0.05 level.

[c] Cost of inbreeding for F = 0.25: $= 1 - \left[\frac{\text{Predicted inbred survival: } e^{-(A+.25B)}}{(\text{Predicted non = inbred survival: } e^{-(A)}}\right] = 1 - e^{-.25B}$

using the average B value (2.3) results in a cost of inbreeding of 0.44. However, the statistic of interest here is the estimate of the expected value of the cost of inbreeding rather than the cost of inbreeding calculated from the expected value of B. We therefore base our discussion on an average cost of inbreeding of 0.33. The distribution of the cost of inbreeding between first degree relatives is shown in Figure 3.

Discussion

The costs of inbreeding varied widely among captive populations. This is not surprising since one would expect populations to differ in their level of susceptibility to inbreeding. However, in many cases, the models fit the data very poorly and only a small proportion of the variance was explained. These variable results probably reflect the heterogeneous data used for the analysis. The available data for the populations surveyed differed in sample size and the range and number of levels of inbreeding. Nevertheless, these results do provide data on the costs of inbreeding and number of lethal equivalents in a wide variety of captive populations and allow analyses of general trends and patterns.

The median number of estimated lethal equivalents for the captive mammalian populations we examined was 3.1. This figure is similar to estimates for other animal populations. Humans (May 1979), *Drosophila* (Dobzhansky 1970), and the great tit, *Parus major* (Bulmer 1973), are thought to have about two lethal equivalents per individual, and the Japanese quail, *Coturnix coturnix japonica*, is thought to have about 3.4 (Sittmann, Abplanalp & Fraser 1986). Our estimates for captive carnivores, although based on only three populations, were quite low. More carnivore populations should be studied to determine if this is characteristic of the order or unique to the data sets we examined.

May (1979), assuming the number of lethal equivalents in humans was 2.2, estimated the cost of breeding in humans at F = 0.25 to be .42. However, his equation for calculating the inbreeding cost contained an error. The correct cost, based on formula (4), is .24. This es-

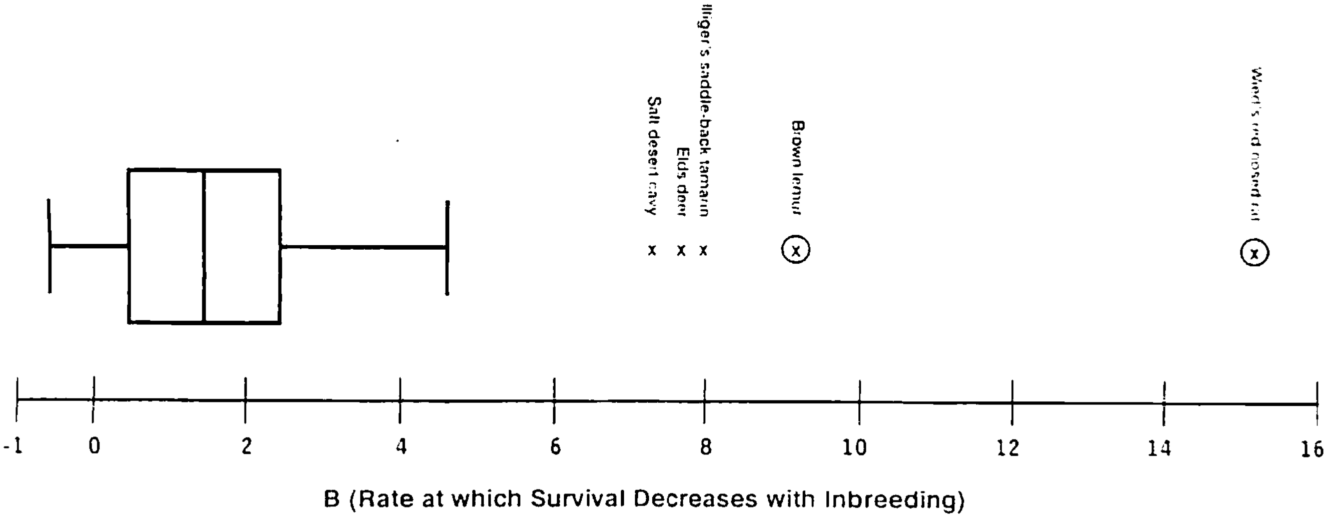

Figure 1. Box plots of B, a measure of the rate at which survival decreases with increasing inbreeding, for 40 mammalian populations. The median (middle vertical line in box), upper and lower quartiles (left and right ends of box), upper and lower inner fences (vertical lines), outlying values (x), and values beyond the outer fences (⊗) are shown (Hoaglin, Mosteller, & Tukey 1983).

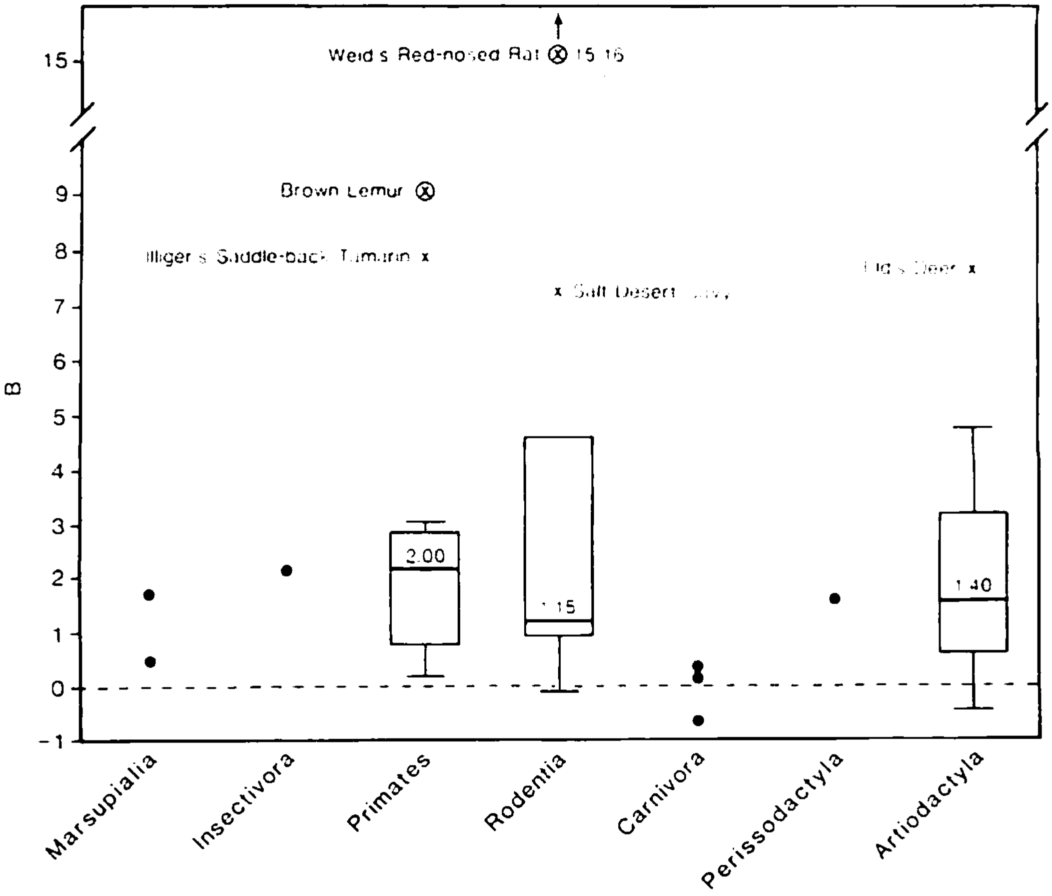

Figure 2. Box plots of B across 40 mammalian populations by order. Median effects (middle horizontal line in box), upper and lower quartiles (upper and lower ends of boxes), upper and lower inner fences (horizontal lines), outlying values (x), and values beyond the outer fences (⊗) are shown for the distribution of B in primates, rodents, and artiodactyls. Results for individual populations in other orders are shown by solid dots.

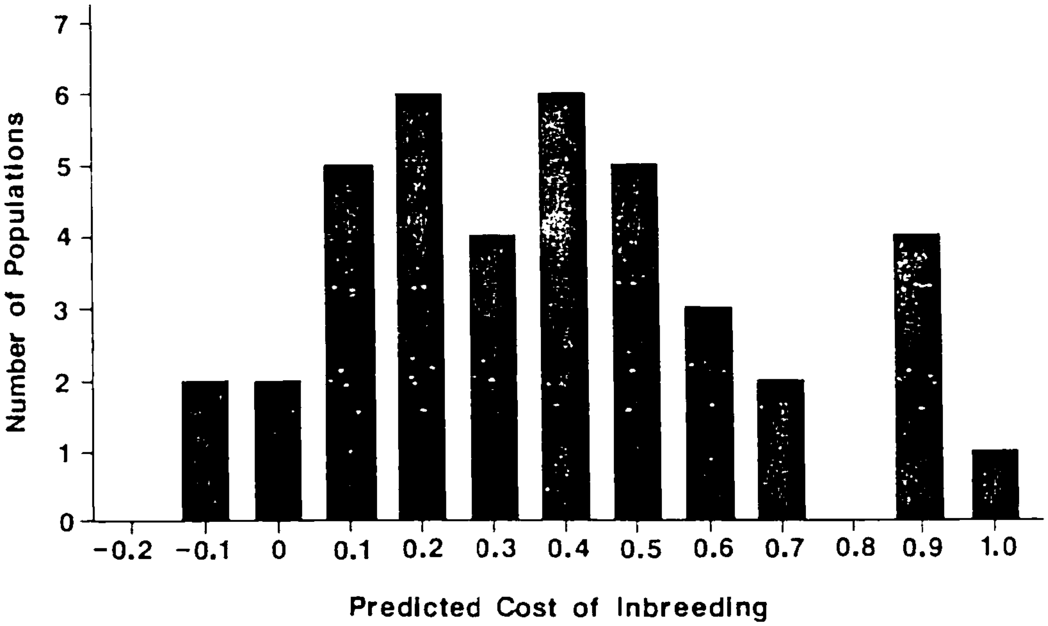

Figure 3. Distribution of the predicted cost of inbreeding in matings resulting in young with an inbreeding coefficient of 0.25 (i.e., matings between parents and offspring or full siblings) for 40 mammal populations.

timate is slightly lower than the average .33 cost of inbreeding found in our mammal populations.

The total costs of inbreeding in natural populations are probably considerably higher than our estimates. First, our estimate of the cost based on only one component of fitness (survival of young) is probably low. We were unable to count early embryonic deaths, exclude individuals with inbred ancestors, and follow individuals until the age of reproductive maturity. Furthermore, mortality rates of inbred young may be higher in natural populations, because many weak young that might die in the wild survive in captivity with the assistance of veterinary care. Second, there are likely to be additional costs of inbreeding in other components of fitness, such as litter size in species that normally bear multiple young and a reduction in fecundity of the inbred young that do survive to reproductive age (Wright 1977). (The reported higher recruitment rate of inbred young in the great tit (van Noordwijk & Scharloo 1981) is not supported by the data (Greenwood & Harvey 1982).) Third, inbred individuals with low levels of heterozygosity may be highly susceptible to viral epidemics (O'Brien et al. 1985).

Considering only the cost of inbreeding relative to the gain in inclusive fitness due to inbreeding, theory suggests that females should not mate with their fathers or sons unless the cost of inbreeding is less than .33 (Smith 1979). Although this is a highly oversimplified model, our data suggest that the cost of inbreeding in mammals is usually high enough (mean = .33) that females should not mate with their closest relatives. The limited data on the frequency of such matings in natural populations of mammals agree with this prediction. Estimates based on observations of identifiable individuals during long-term field studies range from zero to 2% in 9 of 14 well-studied mammalian populations, and the highest documented frequency is 5.5% (Ralls, Harvey & Lyles 1986).

Estimates of the cost of inbreeding also have important applications to conservation biology. The effects of the accelerated rate of inbreeding in small populations, in both captivity and the wild, can potentially drive a population towards extinction (Gilpin & Soulé 1986). The susceptibility of most small populations of conservation interest to elevated levels of inbreeding is unknown, and predicting the degree to which mortality may be increased as a result of inbreeding is impossible. The results presented here provide estimates of the general relationship between the rates of inbreeding and juvenile mortality in a large variety of captive mammal populations and will be useful in developing conservation management programs for small populations (Ballou, in press). Unfortunately, however, our estimates of the cost of inbreeding for individual populations varied greatly and were not clustered near the mean value. Thus, the severity of inbreeding effects in any unstudied mammalian population is quite likely to differ from that predicted by models based on average values.

Acknowledgments

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Essay

Assessing Extinction Threats: Toward a Reevaluation of IUCN Threatened Species Categories

GEORGINA M. MACE
Institute of Zoology
Zoological Society of London
Regent's Park, London NW1 4RY, U.K.

RUSSELL LANDE
Department of Ecology and Evolution
University of Chicago
Chicago, Illinois 60637, U.S.A.

Abstract: *IUCN categories of threat (Endangered, Vulnerable, Rare, Indeterminate, and others) are widely used in 'Red lists' of endangered species and have become an important tool in conservation action at international, national, regional, and thematic levels. The existing definitions are largely subjective, and as a result, categorizations made by different authorities differ and may not accurately reflect actual extinction risks. We present proposals to redefine categories in terms of the probability of extinction within a specific time period, based on the theory of extinction times for single populations and on meaningful time scales for conservation action. Three categories are proposed (CRITICAL, ENDANGERED, VULNERABLE) with decreasing levels of threat over increasing time scales for species estimated to have at least a 10% probability of extinction within 100 years. The process of assigning species to categories may need to vary among different taxonomic groups, but we present some simple qualitative criteria based on population biology theory, which we suggest are appropriate at least for most large vertebrates. The process of assessing threat is clearly distinguished from that of setting priorities for conservation action, and only the former is discussed here.*

Resumen: *La categorización de la Unión Internacional para la Conservación de la Naturaleza (UICN) de las especies amenazadas (en peligro, vulnerables, raras, indeterminadas y otras) son ampliamente utilizadas en las Listas Rojas de especies en peligro y se han convertido en una herramienta importante para las acciones de conservación al nivel internacional, nacional, regional y temático. Las definiciones de las categorias existentes son muy subjetivas y, como resultado, las categorizaciones hechas por diferentes autores difieren y quizás no reflejen con certeza el riesgo real de extinción. Presentamos propuestas para re-definir las categorias en términos de la probabilidad de extinción dentro de un periodo de tiempo especifico. Las propuestas están basadas en la teoria del tiempo de extinción para poblaciones individuales y en escalas de tiempo que tengan significado para las acciones de conservación. Se proponen tres categorias (CRITICA, EN PELIGRO, VULNERABLE) con niveles decrecientes de amenaza sobre escalas de tiempo en aumento para especies que se estima tengan cuando ménos un 10% de probabilidad de extinción en 100 años. El proceso de asignar especies a categorias puede que necesite variar dentro de los diferentes grupos taxonómicos pero nosotros presentamos algunos criterios cualitativos simples basados en la teoria de la biologia de las poblaciones, las cuales sugerimos son apropiadas para cuando ménos la mayoria de los grandes vertebrados. El proceso de evaluar la amenaza se distingue claramente del de definir las prioridades para las acciones de conservación, sólamente el primero se discute aquí.*

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Introduction

Background

The Steering Committee of the Species Survival Commission (SSC) of the IUCN has initiated a review of the overall functioning of the Red Data Books. The review will cover three elements: (1) the form, format, content, and publication of Red Data Books; (2) the categories of threat used in Red Data Books and the IUCN Red List (Extinct, Endangered, Vulnerable, Rare, and Indeterminate); and (3) the system for assigning species to categories. This paper is concerned with the second element and includes proposals to improve the objectivity and scientific basis for the threatened species categories currently used in Red Data Books (see IUCN 1988 for current definitions).

There are at least three reasons why a review of the categorization system is now appropriate: (1) the existing system is somewhat circular in nature and excessively subjective. When practiced by a few people who are experienced with its use in a variety of contexts it can be a robust and workable system, but increasingly, different groups with particular regional or taxonomic interests are using the Red Data Book format to develop local or specific publications. Although this is generally of great benefit, the interpretation and use of the present threatened species categories are now diverging widely. This leads to disputes and uncertainties over particular species that are not easily resolved and that ultimately may negatively affect species conservation. (2) Increasingly, the categories of threat are being used in setting priorities for action, for example, through specialist group action plans (e.g., Oates 1986; Eudey 1988; East 1988, 1989; Schreiber et al. 1989). If the categories are to be used for planning then it is essential that the system used to establish the level of threat be consistent and clearly understood, which at present it does not seem to be. (3) A variety of recent developments in the study of population viability have resulted in techniques that can be helpful in assessing extinction risks.

Assessing Threats Versus Setting Priorities

In the first place it is important to distinguish systems for assessing threats of extinction from systems designed to help set priorities for action. The categories of threat should simply provide an assessment of the likelihood that if current circumstances prevail the species will go extinct within a given period of time. This should be a scientific assessment, which ideally should be completely objective. In contrast, a system for setting priorities for action will include the likelihood of extinction, but will also embrace numerous other factors, such as the likelihood that restorative action will be successful; economic, political, and logistical considerations; and perhaps the taxonomic distinctiveness of the species under review. Various categorization systems used in the past, and proposed more recently, have confounded these two processes (see Fitter & Fitter 1987; Munton 1987). To devise a general system for setting priorities is not useful because different concerns predominate within different taxonomic, ecological, geographical, and political units. The process of setting priorities is therefore best left to specific plans developed by specialist bodies such as the national and international agencies, the specialist groups, and other regional bodies that can devise priority assessments in the appropriate regional or taxonomic context. An objective assessment of extinction risk may also then contribute to the decisions taken by governments on which among a variety of recommendations to implement. The present paper is therefore confined to a discussion of assessing threats.

Aims of the System of Categorization

For Whom?

Holt (1987) identifies three different groups whose needs from Red Data Books (and therefore categories of threat) may not be mutually compatible: the lay public, national and international legislators, and conservation professionals. In each case the purpose is to highlight taxa with a high extinction risk, but there are differences in the quality and quantity of information needed to support the assessment. Scott et al. (1987) make the point that in many cases simple inclusion in a Red Data Book has had as much effect on raising awareness as any of the supporting data (see also Fitter 1974). Legislators need a simple, but objective and soundly based system because this is most easily incorporated into legislation (Bean 1987). Legislators frequently require some statement about status for every case they consider, however weak the available information might be. Inevitably, therefore, there is a conflict between expediency and the desire for scientific credibility and objectivity. Conservationists generally require more precision, particularly if they are involved in planning conservation programs that aim to make maximal use of limited resources.

Characteristics of an Ideal System

With this multiplicity of purposes in mind it is appropriate to consider various characteristics of an ideal system:

(1) The system should be essentially simple, providing easily assimilated data on the risk of extinction. In terms of assessing risk, there seems to be little virtue in developing numerous categories, or in categorizing risk on the basis of a range of different parameters (e.g., abundance, nature of threat, likelihood of persistence of threat, etc.). The categories should be few in number,

should have a clear relationship to one another (Holt 1987; Munton 1987), and should be based around a probabilistic assessment of extinction risk.

(2) The system for categorization has to be flexible in terms of data required. The nature and amount of data available to assess extinction risks varies widely from almost none (in the vast majority of species) to highly detailed population data (in a very few cases). The categorization system should make maximum use of whatever data are available. One beneficial consequence of this process would be to identify key population data for field workers to collect that would be useful in assessing extinction risk.

(3) The categorization system also needs to be flexible in terms of the population unit to which it applies. Throughout this discussion, it is assumed that the system being developed will apply to any species, subspecies, or geographically separate population. The categorization system therefore needs to be equally applicable to limited lower taxonomic levels and to more limited geographical scope. Action planning will need to be focused on particular taxonomic groups or geographical areas, and can then incorporate an additional system for setting priorities that reflect taxonomic distinctiveness and extinction risks outside the local area (e.g., see East 1988, 1989; Schreiber et al. 1989).

(4) The terminology used in categorization should be appropriate, and the various terms used should have a clear relationship to each other. For example, among the current terms both 'endangered' and 'vulnerable' are readily comprehended, but 'rare' is confusing. It can be interpreted as a statement about distribution status, level of threat, or local population size, and the relationships between these factors are complex (Rabinowitz et al. 1986). Rare (i.e., low-density) species are not always at risk and many species at risk are not numerically rare (King 1987; Munton 1987; Heywood 1988). The relationship of 'rare' to 'endangered' and 'vulnerable' is also unclear.

(5) If the system is to be objectively based upon sound scientific principles, it should include some assessment of uncertainty. This might be in terms of confidence levels, sensitivity analyses, or, most simply, on an ordinal scale reflecting the adequacy of the data and models in any particular case.

(6) The categories should incorporate a time scale. On a geological time scale all species are doomed to extinction, so terms such as "in danger of extinction" are rather meaningless. The concern we are addressing here is the high background level of the current rates of extinction, and one aim is therefore preservation over the upcoming centuries (Soulé & Simberloff 1986). Therefore, the probability of extinction should be expressed in terms of a finite time scale, for example, 100 years. Munton (1987) suggests using a measure of number of years until extinction. However, since most models of population extinction times result in approximately exponential distributions, as in Goodman's (1987) model of density-dependent population growth in a fluctuating environment, mean extinction time may not accurately reflect the high probability that the species will go extinct within a time period considerably shorter than the mean (see Fig. 1). More useful are measures such as "95% likelihood of persistence for 100 years."

Population Viability Analysis and Extinction Factors

Various approaches to defining viable populations have been taken recently (Shaffer 1981, 1990; Gilpin & Soulé, 1986; Soulé 1987). These have emphasized that there is no simple solution to the question of what constitutes a viable population. Rather, through an analysis of extinction factors and their interactions it is possible to assess probabilities and time scales for population persistence for a particular taxon at a particular time and place. The development of population viability analyses has led to the definition of intrinsic and extrinsic factors that determine extinction risks (see Soulé 1983; Soulé 1987; Gilpin & Soulé 1986; see also King 1987). Briefly these can be summarized as population dynamics (number of individuals, life history and age or stage distribution, geographic structure, growth rate, variation in demographic parameters), population characteristics (morphology, physiology, genetic variation, behavior and dispersal patterns), and environmental effects (habitat quality and quantity, patterns and rates of environmental disturbance and change, interactions with other species including man).

Preliminary models are available to assess a population's expected persistence under various extinction pressures, for example, demographic variation (Goodman 1987*a, b;* Belovsky 1987; CBSG 1989), catastrophes (Shaffer 1987), inbreeding and loss of genetic diversity (Lande & Barrowclough 1987; Lacy 1987), metapopulation structure (Gilpin 1987; Quinn & Hastings 1987; Murphy et al. 1990). In addition, various approaches have been made to modeling extinction in populations threatened by habitat loss (e.g., Gutiérrez & Carey 1985; Maguire et al. 1987; Lande 1988), disease (e.g., Anderson & May 1979; Dobson & May 1986; Seal et al. 1989), parasites (e.g., May & Anderson 1979; May & Robinson 1985; Dobson & May 1986), competitors, poaching (e.g., Caughley 1988), and harvesting or hunting (e.g., Holt 1987).

So far, the development of these models has been rather limited, and in particular they often fail to successfully incorporate several different extinction factors and their interactions (Lande 1988). Nevertheless the approach has been applied in particular cases even with existing models (e.g., grizzly bear: Shaffer 1983; spotted owl: Gutiérrez & Carey 1985; Florida panther: CBSG 1989), and there is much potential for further development.

Although different extinction factors may be critical for different species, other, noncritical factors cannot be ignored. For example, it seems likely that for many species, habitat loss constitutes the most immediate threat. However, simply preserving habitats may not be sufficient to permit long term persistence if surviving populations are small and subdivided and therefore have a high probability of extinction from demographic or genetic causes. Extinction factors may also have cumulative or synergistic effects; for example, the hunting of a species may not have been a problem before the population was fragmented by habitat loss. In every case, therefore, all the various extinction factors and their interactions need to be considered. To this end more attention needs to be directed toward development of models that reflect the random influences that are significant to most populations, that incorporate the effects of many different factors, and that relate to the many plant, invertebrate, and lower vertebrate species whose population biology has only rarely been considered so far by these methods.

Viability analysis should suggest the appropriate kind of data for assigning extinction risks to species, though much additional effort will be needed to develop appropriate models and collect appropriate field data.

Proposal

Three Categories and Their Justification

We propose the recognition of three categories of threat (plus EXTINCT), defined as follows:

CRITICAL:	50% probability of extinction within 5 years or 2 generations, whichever is longer.
ENDANGERED:	20% probability of extinction within 20 years or 10 generations, whichever is longer.
VULNERABLE:	10% probability of extinction within 100 years.

These definitions are based on a consideration of the theory of extinction times for single populations as well as on meaningful time scales for conservation action. If biological diversity is to be maintained for the foreseeable future at anywhere near recent levels occurring in natural ecosystems, fairly stringent criteria must be adopted for the lowest level of extinction risk, which we call VULNERABLE. A 10% probability of extinction within 100 years has been suggested as the highest level of risk that is biologically acceptable (Shaffer 1981) and seems appropriate for this category. Furthermore, events more than about 100 years in the future are hard to foresee, and this may be the longest duration that legislative systems are capable of dealing with effectively.

It seems desirable to establish a CRITICAL category to emphasize that some species or populations have a very high risk of extinction in the immediate future. We propose that this category include species or populations with a 50% chance of extinction within 5 years or two generations, and which are clearly at very high risk.

An intermediate category, ENDANGERED, seems desirable to focus attention on species or populations that are in substantial danger of extinction within our lifetimes. A 20% chance of extinction within 20 years or 10 generations seems to be appropriate in this context.

For increasing levels of risk represented by the categories VULNERABLE, ENDANGERED, and CRITICAL, it is necessary to increase the probability of extinction or to decrease the time scale, or both. We have chosen to do both for the following reasons. First, as already mentioned, decreasing the time scale emphasizes the immediacy of the situation. Ideally, the time scale should be expressed in natural biological units of generation time of the species or population (Leslie 1966), but there is also a natural time scale for human activities such as conservation efforts, so we have given time scales in years and in generations for the CRITICAL and ENDANGERED categories.

Second, the uncertainty of estimates of extinction probabilities decreases with increasing risk levels. In population models incorporating fluctuating environments and catastrophes, the probability distribution of extinction times is approximately exponential (Nobile et al. 1985; Goodman 1987). In a fluctuating environment where a population can become extinct only through a series of unfavorable events, there is an initial, relatively brief period in which the chance of extinction is near zero, as in the inverse Gaussian distribution of extinction times for density-independent fluctuations (Ginzburg et al. 1982; Lande & Orzack 1988). If catastrophes that can extinguish the population occur with probability p per unit time, and are much more important than normal environmental fluctuations, the probability distribution of extinction times is approximately exponential, pe^{-pt}, and the cumulative probability of extinction up to time t is approximately $1 - e^{-pt}$. Thus, typical probability distributions of extinction times look like the curves in Figures 1A and 1B, and the cumulative probabilities of extinction up to any given time look like the curves in Figures 1C and 1D. Dashed curves represent different distributions of extinction times and cumulative extinction probabilities obtained by changing the model parameters in a formal population viability analysis (e.g., different amounts of environmental variation in demographic parameters). The uncertainty in an estimate of cumulative extinction probability up to a certain time can be measured by its coefficient of variation, that is, the standard deviation among different estimates of the cumulative extinction probability with respect to reasonable variation in model parameters, divided by the best estimate. It is apparent from Figures 1C and 1D that at least for small variations in the parameters (if the parameters are reasonably well known), the uncertainty of estimates of cumulative extinction probability at particular times decreases as the level of risk increases. Thus at times, t_1, t_2, and t_3 when the best estimates of the cumulative extinction probabilities are 10%, 20%, and 50% respectively, the corresponding ranges of extinction probabilities in Figure 1C are 6.5%–14.8%, 13.2%–28.6%, and 35.1%–65.0%, and in Figure 1D are 6.8%–13.1%, 13.9%–25.7%, and 37.2%–60.2%. Taking half the range as a rough approximation of the standard deviation in this simple illustration gives uncertainty measures of 0.41, 0.38, and 0.30 in Figure 1C, and 0.31, 0.29, and 0.23 in Figure 1D, corresponding to the three levels of risk. Given that for practical reasons we have chosen to shorten the time scales for the more threatened categories, these results suggest that to maintain low levels of uncertainty, we should also increase the probabilities of extinction in the definition of the ENDANGERED and CRITICAL categories.

These definitions are based on general principles of population biology with broad applicability, and we believe them to be appropriate across a wide range of life forms. Although we expect the process of assigning species to categories (see below) to be an evolving (though closely controlled and monitored) process, and one that might vary across broad taxonomic groups, we recommend that the definitions be constant both across taxonomic groups and over time.

Assigning Species or Populations to Categories

We recognize that in most cases, there are insufficient data and imperfect models on which to base a formal probabilistic analysis. Even when considerable information does exist there may be substantial uncertainties in the extinction risks obtained from population models containing many parameters that are difficult to estimate accurately. Parameters such as environmental stochasticity (temporal fluctuations in demographic parameters such as age- or developmental stage–specific mortality and fertility rates), rare catastrophic events, as well as inbreeding depression and genetic variability in particular characters required for adaptation are all difficult to estimate accurately. Therefore it may not be possible to do an accurate probabilistic viability analysis even for some very well studied species. We suggest that the categorization of many species should be based on more qualitative criteria derived from the same body of theory as the definitions above, which will broaden the scope and applicability of the categorization system. In these more qualitative criteria we use measures of effective population size (N_e) and give approximate equivalents in actual population size (N). It is important to recognize that the relationship between N_e and N depends upon a variety of interacting factors. Estimating N_e for a particular population will require quite extensive information on breeding structure and life history characteristics of the population and may then produce only an approximate figure (Lande & Barrowclough 1987). In addition, different methods of estimating N_e will give variable results (Harris & Allendorf 1989). N_e/N ratios vary widely across species, but are typically in the range 0.2 to 0.5. In the criteria below we give a value for N_e as well as an approximate value of N assuming that the N_e/N ratio is 0.2.

We suggest the following criteria for the three categories:

CRITICAL: 50% probability of extinction within 5 years or 2 generations, whichever is longer, or

(1) Any two of the following criteria:
  - (a) Total population $N_e < 50$ (corresponding to actual $N < 250$).
  - (b) Population fragmented: ≤ 2 subpopulations with $N_e > 25$ ($N > 125$) with immigration rates < 1 per generation.
  - (c) Census data of $>20\%$ annual decline in numbers over the past 2 years, or $>50\%$ decline in the last generation, or equivalent projected declines based on demographic projections after allowing for known cycles.
  - (d) Population subject to catastrophic crashes ($>50\%$ reduction) per 5 to 10 years, or 2 to 4 generations, with subpopulations highly correlated in their fluctuations.

or (2) Observed, inferred, or projected habitat alteration (i.e., degradation, loss, or fragmentation) resulting in characteristics of (1).

or (3) Observed, inferred, or projected commercial exploitation or ecological interactions with introduced species (predators, competitors, pathogens, or parasites) resulting in characteristics of (1).

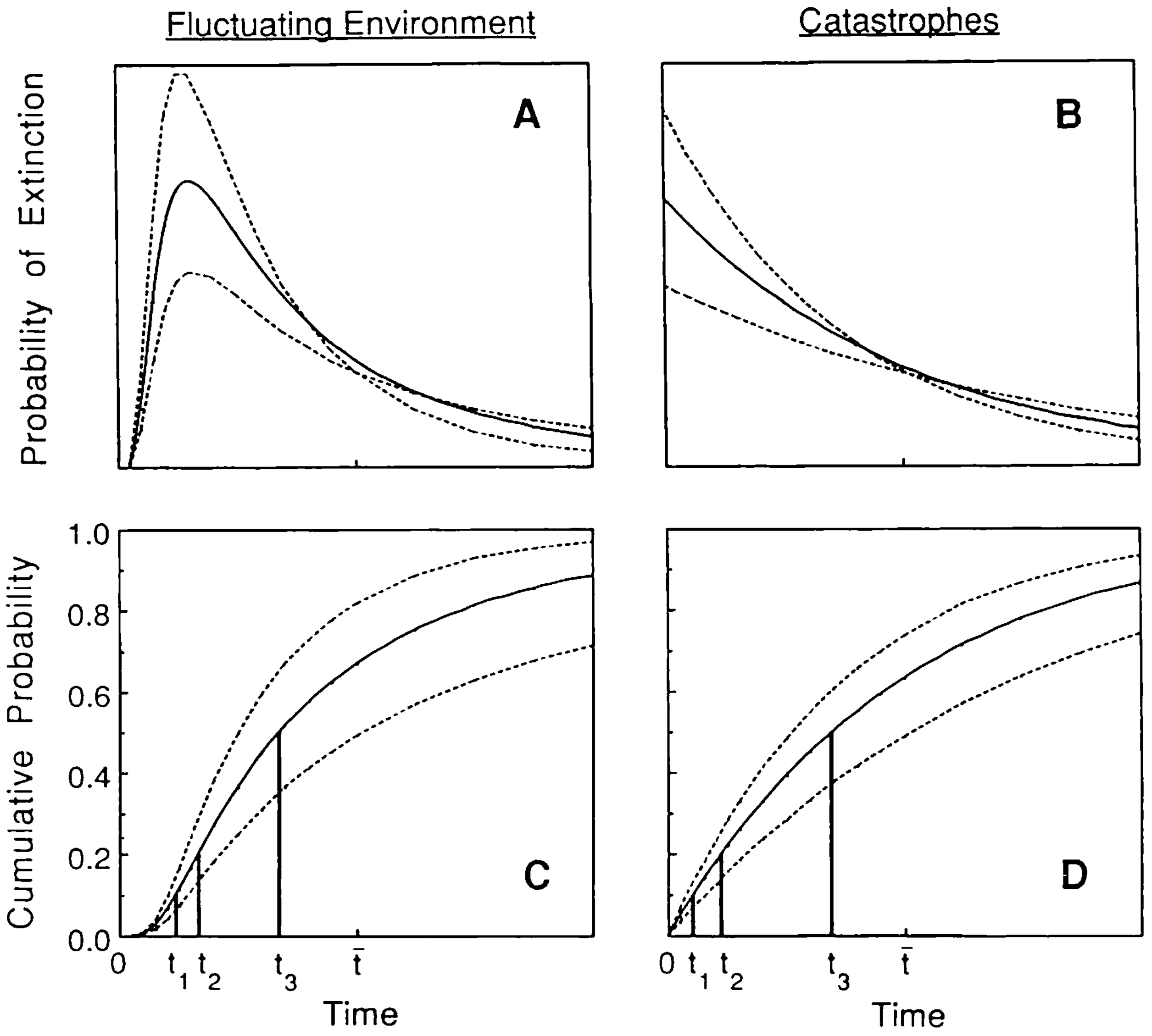

Figure 1. Probability distributions of time to extinction in a fluctuating environment, inverse Gaussian distributions (A), or with catastrophes, exponential distributions (B). Corresponding cumulative extinction probabilities of extinction up to any given time are shown below (C and D). Solid curves represent the best estimates from available data and dashed curves represent different estimates based upon the likely range of variation in the parameters. t_1, t_2, and t_3 are times at which the best estimates of cumulative extinction probabilities are 10%, 20%, and 50%. $\bar{t}$ is the expected time to extinction in the solid curves.

ENDANGERED:

20% probability of extinction within 20 years or 10 generations, whichever is longer, or

(1) Any two of the following or any one criterion under CRITICAL
- (a) Total population $N_e < 500$ (corresponding to actual $N < 2{,}500$).
- (b) Population fragmented:
  - (i) ≤ 5 subpopulations with $N_e > 100$ ($N > 500$) with immigration rates <1 per generation, or
  - (ii) ≤ 2 subpopulations with $N_e > 250$ ($N > 1{,}250$) with immigration rates <1 per generation.
- (c) Census data of $>5\%$ annual decline in numbers over past 5 years, or $>10\%$ decline per generation over past 2 generations, or equivalent projected declines based on demographic data after

allowing for known cycles.

(d) Population subject to catastrophic crashes: an average of >20% reduction per 5 to 10 years or 2 to 4 generations, or >50% reduction per 10 to 20 years or 5 to 10 generations, with subpopulations strongly correlated in their fluctuations.

or (2) Observed, inferred, or projected habitat alteration (i.e., degradation, loss, or fragmentation) resulting in characteristics of (1).

or (3) Observed, inferred, or projected commercial exploitation or ecological interactions with introduced species (predators, competitors, pathogens, or parasites) resulting in characteristics of (1).

VULNERABLE:

10% probability of extinction within 100 years, or

(1) Any two of the following criteria or any one criterion under ENDANGERED.

(a) Total population $N_e < 2,000$ (corresponding to actual $N < 10,000$).

(b) Population fragmented:
(i) ≤ 5 subpopulations with $N_e > 500$ ($N > 2,500$) with immigration rates <1 per generation, or
(ii) ≤ 2 subpopulations with $N_e > 1,000$ ($N > 5,000$) with immigration rates <1 per generation.

(c) Census data of >1% annual decline in numbers over past 10 years, or equivalent projected declines based on demographic data after allowing for known cycles.

(d) Population subject to catastrophic crashes: an average of >10% reduction per 5 to 10 years, >20% reduction per 10 to 20 years, or >50% reduction per 50 years, with subpopulations strongly correlated in their fluctuations.

or (2) Observed, inferred, or projected habitat alteration (i.e., degradation, loss, or fragmentation) resulting in characteristics of (1).

or (3) Observed, inferred, or projected commercial exploitation or ecological interactions with introduced species (predators, competitors, pathogens, or parasites) resulting in characteristics of (1).

Prior to any general acceptance, we recommend that these criteria be assessed by comparison of the categorizations they lead to in particular cases with the results of formal viability analyses, and categorizations based on existing methods. This process should help to resolve uncertainties about both the practice of, and results from, our proposals. We expect a system such as this to be relatively robust and of widespread applicability, at the very least for most higher vertebrates. For some invertebrate and plant taxa, different kinds of criteria will need to be developed within the framework of the definitions above. For example, many of these species have very high rates of population growth, short generation times, marked or episodic fluctuations in population size, and high habitat specificity. Under these circumstances, it will be more important to incorporate metapopulation characteristics such as subpopulation persistence times, colonization rates, and the distribution and persistence of suitable habitats into the analysis, which are less significant for most large vertebrate populations (Murphy et al. 1990; Menges 1990).

Change of Status

The status of a population or species with respect to risk of extinction should be up-listed (from unlisted to VULNERABLE, from VULNERABLE to ENDANGERED, or from ENDANGERED to CRITICAL) as soon as current information suggests that the criteria are met. The status of a population or species with respect to risk of extinction should be down-listed (from CRITICAL to ENDANGERED, from ENDANGERED to VULNERABLE, or from VULNERABLE to unlisted) only when the criteria of the lower risk category have been satisfied for a time period equal to that spent in the original category, or if it is shown that past data were inaccurate.

For example, if an isolated population is discovered consisting of 500 individuals and no other information is available on its demography, ecology, or the history of the population or its habitat, this population would initially be classified as ENDANGERED. If management efforts, natural events, or both caused the population to increase so that 10 years later it satisfied the criteria of the VULNERABLE category, the population would not be removed from the ENDANGERED category for a further period of 10 years. This time lag in down-listing prevents frequent up-listing and down-listing of a population or species.

Uncertain or Conflicting Results

Because of uncertainties in parameter estimates, especially those dealing with genetics and environmental variability and catastrophes, substantial differences may arise in the results from analyses of equal validity performed by different parties. In such cases, we recommend that the criteria for categorizing a species or population should revert to the more qualitative ones outlined above.

Reporting Categories of Threat

To objectively compare categorizations made by different investigators and at different times, we recommend that any published categorization also cite the method used, the source of the data, a date when the data were accurate, and the name of the investigator who made the categorization. If the method was by a formal viability model, then the name and version of the model used should also be included.

Conclusion

Any system of categorizing degrees of threat of extinction inevitably contains arbitrary elements. No single system can adequately cover every possibility for all species. The system we describe here has the advantage of being based on general principles from population biology and can be used to categorize species for which either very little or a great deal of information is available. Although this system may be improved in the future, we feel that its use will help to promote a more uniform recognition of species and populations at risk of premature extinction, and should thereby aid in setting priorities for conservation efforts.

Summary

1. Threatened species categories should highlight species vulnerable to extinction and focus appropriate reaction. They should therefore aim to provide objective, scientifically based assessments of extinction risks.
2. The audience for Red Data Books is diverse. Positive steps to raise public awareness and implement national and international legislation benefit from simple but soundly based categorization systems. More precise information is needed for planning by conservation bodies.
3. An ideal system needs to be simple but flexible in terms of data required. The category definitions should be based on a probabilistic assessment of extinction risk over a specified time interval, including an estimate of error.
4. Definitions of categories are appropriately based on extinction probabilities such as those arising from population viability analysis methods.
5. We recommend three categories, CRITICAL, ENDANGERED, and VULNERABLE, with decreasing probabilities of extinction risk over increasing time periods.
6. For most cases, we recommend development of more qualitative criteria for allocation to categories based on basic principles of population biology. We present some criteria that we believe to be appropriate for many taxa, but are appropriate at least for higher vertebrates.

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THE IUCN POLICY STATEMENT ON CAPTIVE BREEDING

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