(iv) the resources that have already been expended on its conservation, and the interest and willingness of Zaire to conserve the species;

(v) the flagship nature of the species for conservation in this region of Africa.

2. The Workshop recommends Integration of the conservation programs for the wild and captive populations. Ultimately, these programs are expected to entail exchange of genetic material between the wild and captive populations. Fewer than 15 founder animals are known to exist for both the small wild and captive populations. These founders are evenly divided between the wild and captive populations. However, over the short term it is recommended that no animals be exchanged between the wild and captive populations; at this time it is recommended that every effort be exerted to expand the wild and captive populations as rapidly as possible from their small founder bases.

3. The Workshop endorses continued support for the *in situ* conservation programs in Garamba National Park. In particular, the Workshop believes that, in addition to the activity currently occurring, funds should be provided for a field biologist who can be deployed continuously in the Park with the rhinos. Further, the Workshop also strongly recommends that there be an intensive effort to train Zairois biologists to continue with these conservation programs into the future.

4. With respect to expansion of the captive population, the Workshop acknowledges and commends the considerable efforts of Dvur Kralove, in collaboration with the IUCN/SSC CBSG, to enhance the captive breeding program, as reflected in the report and recommendations by CBSG chairman Dr. U.S. Seal and CBSG member Dr. D. Jones, issued after their visit to Dvur Kralove in February 1986. Many of these rec-

ommendations have been implemented, including some reproductive examination of females, the movement of a lone male rhino from London to Dvur Kralove, the initiation of a facility enlargement at Dvur Kralove, and collection of samples for genetic analysis.

However, further analysis and evaluation of both the captive and wild population emphasizes the urgent need to expand the captive nucleus as soon as possible. Concerns over the demographic risks of maintaining the entire captive nucleus in one facility have intensified.

Therefore, the Workshop recommends that Dvur Kralove consider movement of 112 adult animals to another facility with experience in breeding the southern white rhino. Further, the Workshop recommends that Dvur Kralove be requested to suggest a timetable by which, if further reproduction does not occur there, other relocations will be undertaken. The reasons for these recommendations relate to enhancement of reproduction and reduction of demographic risks, as will be explained more fully in a white paper to be prepared over the next few months by Dr. Jones and Dr. Seal.

5. The Workshop encourages the use of the southern white rhino for development of reproductive technology to help the northern white rhino.

6. The Workshop also encourages continued investigation of the genetic and ecological differences between the northern and southern forms. With respect to the genetic studies, both field and zoo programs are encouraged to provide sample materials as requested and where practical to Dr. O. Ryder and colleagues.

AFRICAN RHINO SYSTEMATICS
Session Chairman RAOUL DU TOIT

RATIONALE FOR INVESTIGATIONS OF AFRICAN RHINO SYSTEMATICS

Comments by David Western (New York Zoological Society)

To ensure that efforts to conserve rhinos in the wild as well as in captivity are maintaining the existing genetic diversity of the species, it is necessary to establish the "evolutionarily significant units" within the different species. In the case of the northern white rhino, there has been much debate over whether this""subspecies" is sufficiently different from the southern white rhino to merit the expense and effort required to maintain the last remaining population in the Garamba National Park, Zaire. Funds allocated to conservation of these northern white rhinos might be better spent on initiatives to conserve black rhinos, which have dwindled from about 15 000 at the time when this issue was first debated to a present level of under 4 000. The importance of subspecies designations thus requires critical review in order to assign priorities for rhino conservation action in Africa, but conservation Initiatives need not be delayed while the necessary research is undertaken.

In debating the significance of genetic differences between allopatric groups of rhinos, it is necessary to consider not only the need to maintain the evolutionary potential of the species by preserving overall genetic diversity, but also the need to maintain genetic traits that constitute specific ecological adaptations, allowing some of the rhinos to thrive in

habitats which may be unfavourable for other members of the species. Attitudinal zonation of habitats in East Africa may be one important factor influencing ecological adaptations of rhinos.

A further aspect to consider in strategies for conservation in Africa is the likelihood that the recognition of a certain group of a spectacular "flagship species" as being different to other groups of the same species elsewhere gives Impetus to national and International efforts to save those animals and their habitats — the effort to protect the mountain gorilla in Rwanda has been a case of this—"political" aspect of systematics.

THE EXISTING BASIS FOR SUBSPECIES CLASSIFICATION OF BLACK AND WHITE RHINOS

Summary of presentation by Raoul du Toit (IUCN African Elephant and Rhino Specialist Group)

The efforts of Hopwood (1939) and Zukowsky (1965) in revising black rhino systematics did not greatly Improve the classification since these authorities erected subspecies on the basis of very small numbers of representative skulls, and in some Instances the skulls representing their subspecies were those of immature animals (notably the subspecies *holmwoodi).* In view of these deficiencies, Groves (1967) produced a revision which identified 7 subspecies, but sam-

ple sizes were still very low (only 2 of these subspecies were based on measurements of more than 10 adult skulls). Groves' breakdown was as follows (with sample sizes indicated in brackets):

Diceros bicornis b/corn/s (5) South Africa ——Cape area;

D.b. chobiensis (4) Southern Angola, Chobe area;

D.b. minor (23) South Africa to Kenya;

D.b. michaeli (22) Kenya and Tanzania;

D.b. ladoensis (6) Northern Kenya and Sudan;

D.b. longipes (4) Central Africa;

D.b. brucii (10) Somalia and Ethiopia.

Confusion was introduced since Groves did not indicate in this paper that he believed his subspecies *bicornis* to be extinct. This was only made clear in a paper he co-authored with Rookmaker in 1978. Here they stated that *bicornis* was a very large rhino that was exterminated in Namibia and the Cape in about 1850.

Several zoologists continued to refer to *bicornis* as one of the surviving species in southern Africa. Ansell (1978), in his Mammals of Zambia, excluded *bicornis* but had previously stated (1974) that some living rhinos of southern Africa were of this subspecies, and in his recent work Smithers (1983) apparently follows Ansell's original classification; he states that *bicornis* occurred widely in the subcontinent and now has a restricted distribution (presumably meaning this to be Zululand), while he thought *minor* may occur in northern Namibia/Angola (he does not clarify how this fits in with *chobiensis).*

Joubert (1970) compared some Namibian rhino skulls with a sample from Natal. He may not have checked that all skulls were of fully-grown animals, but found that all the Namibian skulls were significantly greater than those from Natal. However, he calculated that the differences between the populations were below the level conventionally accepted for subspecies differences (i.e. the ranges of dimensions had more than 10% overlap) and said all the skulls were of the *bicornis* subspecies.

Rookmaker and Groves (1978) commented that *bicornis* (as described by them from Cape specimens) was similar to *chobiensis* in that both had large skulls, and postulated that this was due to independent adaption to similar (wet) environments. This is clearly fallacious, since the climates of southern Angola/Chobe and the Cape/Namibia are dissimilar, and are not wet.

Thus, the published literature contains rather confusing statements on black rhino taxonomy, and sample sizes are small. Dr. C. Groves recently sent the African Elephant and Rhino Specialist Group (AERSG) an outline of his current ideas on the topic, including data from a few more skulls. His new, interim classification is similar to that he published in 1967, but excludes *bicornis* as an extant subspecies, and has the following criteria for the taxonomic divisions: presence or absence of crista (a tooth feature), greatest length of skull, zygomatic breadth, toothrow length and occipital breadth. Three of the subspecies still have less than 10 representative skulls *(chobiensis, ladoensis* and *iongipes).*

In view of the poor state of black rhino systematics, AERSG Initiated a survey of black rhino skulls in African wildlife areas and in some museums. This survey is not complete, but initial results can be presented. The data indicate that there is statistically significant variation between certain dimensions of female skulls and the equivalent dimensions of male skulls from the same population (notably in toothrow, basilar

length and zygomatic breadth). Groves' latest classification is not supported by the data; for instance, all the skulls that were measured In Etosha National Park have occipital breadths greater than the maximum range indicated by Groves (which was for *chobiensis).* The range in toothrow length which Groves gives for *brucil* totally covers the range he gives for *minor* and thus would be a poor distinguishing feature anyway), but there are a number of fully-grown skulls measured recently from supposed *minor* populations which have even shorter toothrow lengths.

The 300 skulls measured so far in the AERSG survey are mainly from southern Africa and thus only a very tentative conclusion can be reached on the clinal variation in black rhinos. This conclusion is that there may be possibly a trend of decreasing skull size towards the north of the continent, with the largest skulls being from the Namibia animals, a range of Intermediate sized skulls extending up to Kenya and possibly west from there to the Central African Republic, and small skulls from the population to the horn of Africa (Somalia and Ethiopia; where in fact the animals may be effectively exterminated by now). If there is a large-skulled rhino group in Namibia, this may well have been linked with the supposed *bicornis* population as well as with the *chobiensis* population; based on collection localities of skulls designated as *bicornis,* and on ecological similarities between the postulated range of *bicornis,* and that of the extant Namibian rhino, Hail-Martin (1985) has also suggested that these may be the same race.

Thus, in general, it would appear that taxonomic distinctions between black rhinos have been exaggerated and a concerted effort to measure more skulls is justified (the AERSG survey will now build up data from East Africa, but it is expected that few data will be forthcoming from Central Africa). The working premise of AERSG that efforts to conserve rhinos and to create captive breeding groups should concentrate on rhinos from either end of their current range in Africa and from the middle of the distribution is supported. It is also clearly important to undertake further investigations of the ecological adaptions (physiological and behavioural) which suit rhinos to particular environments (notably the Namibian desert and Kenyan highlands) ——adaptions to blood parasites may be particularly important, and would not be revealed by the classical taxonomic approach of measuring skulls.

There has been consensus between taxonomists in the identification of the two subspecies of white rhinos:—*Ceratotherium simum cottoni* and *C.s. simum.* However, these subspecies have been nominated largely on the basis of geographical separation ——several taxonomists have noted that on the basis of skull characteristics the two are not well differentiated. Groves (1972;1975) feels that the major difference is that *simum* has a much deeper dorsal concavity (the occipital crest is raised higher). There is an overlap of only 5% in the ranges of this dimension for the two groups thus the difference, taken in isolation, could be said to constitute a valid subspecies distinction (but, as with the black rhinos, the sample sizes were small ——less than 1 0 *simum* skulls were measured). On the basis of the less indented skull of *cottoni,* Groves (1975) postulates that this subspecies has evolved further than *simum;* he believes that the fossil record indicates an advance from *Diceros* via *C. praecox* to *C. simum* with the dorsal outline of the skull becoming flatter.

The other major skull difference between the subspecies is in toothrow length, with *s/mum* having a longer toothrow, but the coefficient of difference is too small for taxonomic separation on this character (there is an overlap in the ranges of

20%). Alexander and Player (1965) have also stated that the southern race, *simum,* has sparse body hair white the northern has no hairs, only follicles. Groves (1975) suggests that the northern may be longer-legged and shorter-bodied than the southern, but this is not based on any data.

A BRIEF PALAEONTOLOGICAL HISTORY AND COMPARATIVE ANATOMICAL STUDY OF THE RECENT RHINOS OF AFRICA

Summary of presentation by Claude Guerin
(Universite Claude Bernard ——Lyon)

Information on this subject has been published by Guerin (1980).

The black rhino (*Diceros bicornis*)

The lineage begins in the upper part of the middle Miocene, about 12 million years ago, with
Paradiceros mukirii known from Fort Ternan (Kenya) and Beni Mellal (Morocco). The genus *Diceros* appears later in the upper Miocene and is known at that time in Spain, Greece and Turkey with *D. pachygnathus,* In Turkey with *D. neumayri,* and in Tunisia and Italy with *D. douariensis.* The first of these three very large Miocene species may be the ancestor of the white rhino, *Ceratotherium.*

The species *D. bicornis* appears during the Pliocene about 4 to 5 million years ago, and is known in more than 20 sites of Pliocene up to middle Pleistocene age, especially Hadar (Afar) in Ethiopia, Omo (Mursi, Usno and Shungura formations) in Ethiopia, East Turkana in Kenya, Laetolil and Olduvai In Tanzania. More sites of upper Pleistocene and Holocene age are recorded. However, the material is always rare and the fossil form has not yet received any precise taxonomic status. Anatomical differences between the fossil and extant forms are minimal. Thus the fossil form warrants no more than a subspecific status.

I have studied about 60 adult skulls and more than 30 postcranial skeletons of *D. bicornis,* most of these being of Groves' (1967) medium-sized East African forms: subspecies *ladoensis, michaeli* and *brucii.* It is not easy to distinguish between these subspecies, whereas *minor* appears to be smaller-skulled and *bicornis* exceptionally large-skulled. I have not been able to study *chobiensis* and *longipes.* Statistical analyses show that, from the data I collected, *D. bicornis* is homogeneous, with rather normal variability (see Guerin, 1980). The various subspecies appear to constitute a complicated cline.

The white rhino *(Ceratotherium simum)*

The lineage of the white rhino Is much more recent than that of the black. The genus
Ceratotherium appears during the Pliocene with *C. praecox,* a species defined in 1972 by Hooijer and Patterson with material from Kanopol and Ekora in East Africa. The same year Hooijer described abundant material of the same species from Langebaanweg In South Africa. I have studied the material from Chemeron formation (Lake Baringo) and a good deal of material from Hadar (Ethiopia) and from Laetolil (Tanzania). The species is now known in 11 localities of East and South Africa.

The recent species *C. simum* appears about 3 million years ago. it is classically held that there are two fossil subspecies, C.s. *germanoafricanum* from East Africa and *C.s. mauritanicum* from North Africa. I have studied material of *germanoafricanum* from Afar, East Turkana, Olduvai, Omo, Rawi and sever minor locations, and *mauritanicum* material from Ternifine (0.8 million years), Ain Hanech (1.5 mIllion years) and other minor localities. The postcranial material shows clear differences between the fossil and the recent subspecies.

For the two recent forms, *simum* and *cottoni,* I have been able to find only about 30 skulls and 12 postcranials, and many were without specified origin. In fact, only 16 skulls and 8 postcranial skeletons were certainly from *cottoni,* and 8 skulls with 2 postcranial skeletons from *simum.* Hence the results are little more than an indication of differences. On average, *simum* has a skull slightly larger than that of cottoni, with a lower and broader skull roof, and a differently-shaped occipital surface (confirming observations of Groves, 1975). Comparison of fossil forms with the complete sample of recent species shows that the skull of *C. praecox* Is shorter, broader and lower, while the skull of *C.s. germanoafricanum* seems like that of a gigantic white rhino with comparatively narrower occipital surfaces, broader cheek teeth and correspondingly narrower palate widths. A comparison of limb elements again shows *germanofricanum to* be like a giant white rhino, while *mauritanicum* has similar (or exaggerated) proportions to *C. praecox,* being dissimilar to recent white rhinos and *germanoafricanum.*

Since the two Pleistocene subspecies seem to be very different to each other and from the recent ones, *germanoafricanum* probably deserves full species rank and may be the ancestor of the two recent forms; *mauritanicum,* which has no descendants, seems closer to their common ancestor, *C. praecox,* and probably also deserves species rank. The two recent subspecies are clearly distinct from each other and seem to be In the course of a speciation process. More postcranial material, particularly from southern Africa, Is required to help verify this.

BIOCHEMICAL INVESTIGATIONS OF RHINO SYSTEMATICS

Summary of presentation by Matthew George
(Howard University)

A comparative study was undertaken of genetic differences between individual northern and southern white rhinos, and a black rhino. This study was based on comparisons of mitochondrial DNA (mtDNA), which is a useful means of Investigating closely related species since 1.) the molecule Is maternally Inherited, thus complications arising from paternal contributions and recombination events (which affect nuclear DNA) are avoided; 2.) the molecule evolves very rapidly (5-10 times faster than nuclear DNA) so that if differences exist between races they are more likely to be detected than through other methods.

After purification of mtDNA molecules extracted from liver and spleen tissue of the three animals, these were subjected to digestion by 21 different restriction enzymes (which cut the mtDNA at specific sequences of nucleotide units). The cleaved fragments were separated electrophoretically. With most of the restriction enzymes, the migration patterns of mtDNA of the black rhino were different to those of the two white rhinos, while comparison of the two white rhinos showed 13 patterns to be identical and the remaining 8 different.

Analysis of these data indicate that the white rhinos differ by 4% In their nucleotide sequence and they both differ by 7% from the black rhino, If rhinoceros mtDNA changes at a rate of 2% per million years as has been shown in primate mtDNA, the divergence time between the white rhinos is 2 million years, and between either of the white rhinos and the black

rhino is 3.5 million years. The estimated time of divergence between the two species agrees well with fossil evidence (Hooijer, 1969), but the two million year divergence time for the two geographically separated subspecies is surprising; the mtDNA analysis suggests that little or no gene flow has occurred between the races for this period.

The intraspecific variation in mtDNA observed here in the white rhino is consistent with levels of intraspecific variation found in other species such as macaques, apes, rodents, sheep and goats. The intergeneric difference (7%) for the mtDNA of *Ceratotherium* and *Diceros* is somewhat lower than observed in mtDNA studies on other taxa.

We may tentatively conclude that, whereas morphological divergence between *simum* and *cottoni* has been slow (due perhaps to similar selection pressures or convergent evolution), the mtDNA analysis exposes significant genetic differences in these two forms. A second *C.s. simum* individual's mtDNA was subsequently studied, with essentially similar results. However, more sampling is required, in particular to verify the basic level of intraspecific variation in a particular race of white rhino, so that we can be certain that the differences between the northern and southern races are not in fact normal intraspecific polymorphic differences. in addition to increasing the sample size (ideally about 10 rhino from each race should be studied), the number of restriction enzymes could also be increased. *Comments by Oliver Ryder (Zoological Society of San Diego)* While the analysis of mitchondrial DNA of northern and southern white rhinos displays clear differences, no significant differences have been elucidated from protein electrophoretic studies carried out at the University of California, San Diego (A. Merenlender and D._Woodruff). Twenty-six presumptive loci were examined from five northern white rhinos, 14 southern white rhinos and five black rhinos (all *michaeli*). The electrophoretic difference between the northern and southern forms was approximately one-tenth that between white and black rhinos, whereas the. mitochondrial DNA studies had shown a difference between the northern and southern races which was about one-half of the mitochondrial DNA differences between the white and black rhinos.

Additional samples of northern white rhinos have been obtained from animals in captivity at Dvur Kralove, Czechoslovakia and will be subjected to mitochondrial DNA analysis. Additionally, chromosome studies of both black and white rhinos are very limited and should be undertaken. Both of these projects are underway in research supported by the Zoological Society of San Diego and the Ellen B. Scripps Foundation.

The phylogenies derived from fossil, electrophoretic, and mitochondrial DNA studies agree, but questions arise over the rates of evolution and times of divergence between the taxa. It is known that the rates of divergence in different animal lineages vary greatly and it would seem that the genetic loci studied by protein electrophoresis may have a particularly slow rate of evolution in rhinos in comparison to other vertebrates. This is consistent with the mitochondrial DNA findings. The fact that the protein electrophoretic studies indicate that genetic distances between the northern and southern white rhino are no more than those that can be expected in a single randomly mating population, while the mitochondrial DNA studies indicate longstanding genetic isolation, may be due to the difference in rates of evolution of nuclear genes (assayed by protein electrophoresis) a mitochondrial DNA or they may be due to a rehybridization event. Limited breeding occurring between rejoin populations that had been sepa-

rated for some time has led merging of nuclear genes with retention of mitochondial DNAs of only a single population. Generally, the phenomena require recent genetic interaction of the previously separated populations.

While conservation decisions may need to be ma immediately, a clearer understanding of the systematics both white and black rhinos will require further studies chromosomes, protein electrophoresis, mitochondrIal a nuclear DNA genes.

Comments by Don Melnick (Columbia University)
In applying genetic methods to conservation goals we must be careful to avoid placing too much importance on subspecies designations and, instead, assess the distribution of genetic, morphological and ecologic variation throughout a species' range. It is these variants that we wish to conserve in the most efficient, cost-effective w and not the somewhat arbitrary taxonomic distinction between so-called subspecies.

With this in mind, it is necessary to investigate the distribution of genetic diversity (Nel, 1973) across the remaining black rhinoceros populations, in order to establish how much of the species variability can be attributed differences within populations as opposed to difference between populations. This will help us avoid some of the difficulties which have arisen in interpreting the results oft white rhino studies.

The relevance of genetic diversity analysis to rhino conservation in Africa can be Illustrated by an example of two Asian primate species (Melnick, 1987). Only 5% of the genetic diversity found among rhesus monkeys across Asia can be attributed to differences between animals in different regions. The remaining 95% of species diversity is intrapopulation diversity that can be found in any single region. In contrast, 41% of the genetic diversity found among long-tailed macaques can be attributed to difference between regional populations of this species. Hence, if the strategy were devised to conserve the greatest amount on genetic diversity in these primates it would entail the conservation of many more regional populations of the long-tailed macaque than the rhesus monkey. Given the scarcity of resources available for the conservation of the black rhino, we need to determine which of these two types of genetic structure exist.

With the assistance of the New York Zoological Society, the AAZPA and the AERSG, a genetic survey of the black rhino has commenced, with the aim of analyzing mtDNA and bloc proteins in reasonably-sized samples from populations different parts of Africa. Thus far, blood samples from 3 individual black rhinos have been collected in Zimbabwe by P. du Tout, sampling is underway in Kenya and some samples may also become available from South Africa. Sampling very opportunistic, since it usually depends on translocation exercises. It may be very difficult if not impossible to get samples from central Africa. In addition to the wild-caught rhinos, we have collected, with the help of participating zoo blood samples from 12 captive rhinos of Kenyan origin. protocol for tissue collection has been developed and ha been circulated to those who may be in a position to obtain samples.

ECOLOGICAL ADAPTIONS OF RHINOS

Summary of discussion
N. Owen-Smith noted that the feeding ecology of northern white rhinos may well differ to that of the southern white rhinos. The latter graze on short, nutritious grasses while the northern animals live in a wetter habitat, with long fibrous grasses. K. Hillman-Smith confirmed that this is a possibility but relevant research has not yet been undertaken in Garamba National Park. Casual observations indicate that

the northern rhinos may eat more dicotyledons than the southern, and they have to survive in tall grasses he such as *Hyparrhenia* and *Loudetia* in the wet season, and in burnt areas during the dry season. Their social behaviour appears similar to that of the southern rhinos although ranges are about 10 times larger; this may be due to the very low population density in Garamba.

It was generally agreed that estimations of divergence times, subspecies designations and other phylogenetic/taxonomic aspects do not necessarily allow us to identify "evolutionary significant units" (ESU's). Important ecological adaptations may remain hidden from biochemists investigating genetic material and blood proteins, and will almost certainly not be picked up through skull measurements, so it is necessary to investigate the range of habitats in Africa (with their varying selection pressures) in order to outline common-sense strategies for both continental and national rhino conservation initiatives. If a group of rhinos from one part of the species' range is not likely to adapt to different environmental factors when moved to another part of the range, then it is obviously important to conserve representatives of the original populations of both regions.

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APPLICATION OF DECISION ANALYSIS TO BLACK RHINOS
Discussion Leader LYNN MAGUIRE

INTRODUCTION
Purpose

The presentation had three purposes: (if) to introduce several issues crucial to the management of small wild or captive populations; (ii) to propose for discussion some strategies for the coordinated management of wild and captive populations of black and white rhinos; and (ill) to examine two elements of the proposed strategies using formal methods for decision making under uncertainty. These methods have proved useful in developing management plans for other endangered species, including black-footed ferrets (Maguire, 1987a) and tigers (Maguire, 1987b).

Small population management

Several features of the demography and genetics of small populations have important implications for their management.

(I) The concept of *minimum viable population size* (MVP) (Schaffer, 1981) suggests that populations cannot be self-sustaining below some minimum level. Small populations are particularly vulnerable to extinction due to stochastic fluctuations: demographic (e.g. sex ratios at birth), environmental (e.g. variations in food supply), catastrophic (e.g. fire), and genetic (e.g. fixation of deleterious alleles).

(ii) Due to nonrandom mating systems, unequal family sizes, fluctuating population size, and other factors, real populations have an *effective population size* (N_e) that is often far lower than census size, which means that genetic variation Is lost much faster than would appear on the basis of total numbers. Loss of genetic variation is a concern because variation is the raw material for short and long term fitness, in the wild and in captivity.

(iii) Although a relatively small number of founders can capture most of the variation from a larger population initially, this variation will be lost quickly if the population stays small. Black rhinos have declined quickly, suggesting that the remaining animals may provide a good sample of previous levels of genetic variation, but not for long.