

## GENETIC VARIATION IN THE GREATER ONE-HORNED RHINO AND IMPLICATIONS FOR POPULATION STRUCTURE

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### INTRODUCTION

Three generalizations relevant to rhinoceros conservation have emerged from studies measuring genetic diversity in populations of other taxa. These generalizations are that 1) small, abundant organisms typically have more genetic variability than large, rare organisms (Selander and Kaufman, 1973; Powell, 1975; Soule, 1976; Nevo *et al.*, 1984), 2) populations which have experienced severe restrictions in population size (bottlenecks) have low genetic diversity (Bonnell and Selander, 1974; Pemberton and Smith, 1985; O'Brien *et al.*, 1983, 1987; O'Brien and Evermann, 1989), and 3) populations of large mammals tend to have lower variability than smaller mammals (Allendorf *et al.*, 1979; Simonsen *et al.*, 1982a,b; Simonsen, 1982; Manlove *et al.*, 1980). The first generalization is supported by a large amount of empirical data and has been viewed as consistent with expectations of both neutral (Soule, 1976; Kimura, 1983) and selection models (Selander and Kaufman, 1973; Powell, 1975; Nevo *et al.*, 1984). The second generalization also is supported by numerous examples (Bonnell and Selander, 1974; O'Brien *et al.*, 1987; Pemberton and Smith, 1985), and follows from the statistical necessity that, in the absence of selection, heterozygosity will decay at a rate of approximately  $1/2N_e$  per generation (where  $N_e$  is the genetically effective population size); Allendorf, 1986; Lande and Barrowclough, 1987). The third generalization may simply be a correlate of the first generalization because large body size in mammals correlates with a variety of demographic characteristics (e.g., rarity, low fecundity, long generation time; Eisenberg, 1981) which are expected to retard the accumulation of genetic diversity. Recent data (e.g., Baccus *et al.*, 1983; McClenaghan and O'Shea, 1988; Winans and Jones, 1988; Dinerstein and McCracken, 1990) and reevaluations of data (Baccus *et al.*, 1983; Wooten and Smith, 1985), have tended to undermine the empirical basis of this third generalization.

Recently, Dinerstein and McCracken (1990) examined genetic diversity in the population of greater one-horned rhinoceros (*Rhinoceros unicornis*) in Royal Chitwan National Park, Nepal. The biology of these large mammals and their recent severe reduction in numbers led to the a priori expectation that this population would carry very little genetic diversity. However, the estimated levels of heterozygosity ( $H_o = .099$ ) and polymorphism ( $P = .32$ ) in this population were extremely high when compared to values generally observed in other mammals (Table 1). Dinerstein and McCracken (1990) offered an idiographic explanation for the accumulation and retention of high genetic variability in Chitwan *R. unicornis*. They also proposed that the results of their study on *R. unicornis* are an illustration of a current tendency in the conservation literature to overemphasize the importance of population bottlenecks.

In this paper, we review arguments as to why we should expect Chitwan *R. unicornis* to carry high levels of genetic variability. We also argue from data on other taxa, and with consideration of the generalizations given above, that the situation observed for *R. unicornis* is likely to apply to other species, as well. Finally, we consider available data on the levels of genetic variability that are carried in other species of rhinoceros, within the context of these arguments.

## GENETIC DIVERSITY IN *R. UNICORNIS*: THE SPECIES-SPECIFIC SCENARIO

Heterozygosity ( $H_o$ ) is increased by mutations and by gene flow between local populations. Balancing selection will preserve  $H_o$  at the selected loci and other loci in linkage disequilibrium with them (Alledorf, 1986). Genetic drift (sampling error of alleles) and directional selection will reduce  $H_o$ . However, for most loci at most times genetic drift will be the major force reducing heterozygosity (Gilpin, 1991). The effects of genetic drift in finite populations are major concerns in conservation biology.

In explaining the existence of high genetic variability in *R. unicornis*, Dinerstein and McCracken (1990) reviewed aspects of their life history and the historical demography of the Chitwan population. First, it is argued that *R. unicornis* can achieve very high densities in appropriate habitat, that they have high vagility, and that until ca. 1400 AD, they probably maintained  $N_e$ 's of 10's of thousands within their historic range (Fig. 1). The persistence of such large populations, could allow for the accumulation of high  $H_o$  in this taxon. Since ca. 1400 AD, the major causes of their decline were land clearing and hunting by humans, which fragmented the range of *R. unicornis* and greatly reduced their numbers. By the late 19<sup>th</sup> century, populations persisted in only a few isolated areas. However, human encroachment in Chitwan Valley, Nepal was limited until 1950 by a virulent strain of malaria, and until 1950 Chitwan Valley maintained a population of > 1000 *R. unicornis*. Following malaria eradication in 1950 and the movement of humans into the area, land clearing and poaching reduced this population to a low of 60 - 80 survivors in 1962. Effective protection of Chitwan *R. unicornis* by His Majesty's Government of Nepal began in 1962, and by 1988 the Chitwan population had recovered to approximately 400 individuals.

From the results of field studies, Dinerstein and McCracken (1990) estimated that  $N_e$  for *R. unicornis* is approximately equal to  $.35xN$  (where  $N$  = total population size) and that average generation time is about 12 years. Using these values, they calculated the expected decay of  $H_o$  in the Chitwan Valley from 1400 AD to present. From these calculations, Dinerstein and McCracken (1990) estimated that Chitwan *R. unicornis* should still retain approximately 91% of their pre-1400 AD heterozygosity, and high  $H_o$  in this population is not surprising.

### CAN THE *R. UNICORNIS* SPECIFIC CASE BE GENERALIZED?

Major erosion of  $H_o$  within a population will occur when bottlenecks are very small and repeated or sustained over many generations (Nei *et al.*, 1975; Chakraborty *et al.*, 1980; Lande and Barrowclough, 1987; McCommas and Bryant, 1990). Dinerstein and McCracken (1990) argue that high  $H_o$  persists in Chitwan *R. unicornis* because their population size remained large until recently, the genetic bottleneck was recent and of short duration, and their generation time is long. Because many other threatened species, including other rhinoceros, also have long generation times and recent demographic histories that are similar to *R. unicornis*, we suspect that many of these species also have not, as yet, lost substantial portions of their heterozygosity as a result of man's recent impact. It also seems apparent from its trajectory in 1962, that without the timely protection of the Chitwan population it would have become extinct, while still carrying high heterozygosity. Therefore, we feel that these results can be generalized to many other species for which numbers have been rapidly and recently reduced by man's activities, and we concur with recent arguments (Lande, 1988; Pimm *et al.*, 1989) that the importance of bottlenecks to the conservation of threatened species often is overemphasized.

A fourth generalization that emerges from studies estimating levels of genetic variation is that the amount carried in different populations varies enormously. While surveys of many mammal species have converged on an average  $H_o$  of about .04 for mammals (Table 1), the range of values in populations of different species extends from 0 to almost .20 (Nevo *et al.*, 1984). A substantial range in  $H_o$  also can be observed in different populations of the same species (Simon and Archie, 1985), as is illustrated on Table 2 for five local

populations of white-tailed deer. In these populations, estimated levels of heterozygosity range from well above to well below the mammalian average. Although high variation was found in the Chitwan population of *R. unicornis*, this may not be the situation for other remaining populations. In an examination of three *R. unicornis* (2 unrelated individuals) from the only other substantial remaining population of this species (Kaziranga National Park, Assam, India), Merenlender *et al.* (1989) reported no heterozygosity. Whether this result is an artifact of the very small number of individuals examined can only be assessed by examining larger numbers of individuals from this population. The results of a more thorough examination of the Kaziranga population may affect generalizations from the scenario which Dinerstein and McCracken (1990) propose for the Chitwan population.

An extensive review of genetic variation in other mammals is beyond the scope of this paper; however, a very brief consideration of variability in selected other species seems appropriate. Populations of several other species of large mammals also are known to carry levels of genetic diversity that are above the average for mammals (Table 3). Among these, above average variation has been reported for the Florida Manatee, Dall's porpoise, and Minke whale. The high variation in all of these taxa have been attributed to sustained large population sizes and/or high vagility, factors that are thought to be important for *R. unicornis*, as well. In contrast, there also are a large number of populations of other large mammals which carry levels of variation below the mammalian average. Well-known examples include northern elephant seals (Bonnell and Selander, 1974), cheetahs (O'Brien *et al.*, 1983, 1987), and British fallow deer (Pemberton and Smith, 1985). In each of these cases, low  $H_o$  has been attributed to genetic bottlenecks. However, there also are examples of species which apparently have not experienced bottlenecks and which also carry low  $H_o$  (Table 4). Notable in the present context is that low  $H_o$  was found in eight studies on different species of pinnipeds (summarized by Testa, 1986). Excluding northern elephant seals,  $H_o$ 's in these pinniped species ranged from .009 to .033 (mean = .022). Testa (1986) notes that these species are characterized by polygyny and philopatry to specific breeding areas; characteristics that should reduce  $N_e$  and limit gene flow between breeding populations. Southern elephant seals have become a well known example of a species which experienced a genetic bottleneck, and probably lost genetic variation as a consequence (Bonnell and Selander, 1974). However, it seems likely that because of these aspects of their population structure, their populations may have had very little variation even before their numbers were depleted by man's hunting. Testa (1986) emphasizes the need to examine  $H_o$  in other pinnipeds, specifically pack ice breeders which do not have polygynous, fragmented breeding populations.

White-tailed deer were given as an example of a taxon showing substantial variation in  $H_o$  among different populations (Table 2). However, most populations of white-tailed deer that have been examined do carry high  $H_o$  (Tables 2 & 3). White-tailed deer populations often have small  $N_e$ 's, and the variability they carry cannot be readily explained by same factors implicated for Indian rhinos, manatees, and cetaceans. In the case of white-tailed deer, high variability has been attributed to migration between populations, heavy hunting on adult males which may reduce inbreeding and promote dispersal, and to balancing selection (Smith *et al.*, 1984; Sheffield *et al.*, 1985). High variability in other species which are heavily hunted such as red and brockett deer (Smith *et al.*, 1986) may also be at least in part a consequence of one or more of these factors. As reflected in the review papers cited in Table 1, there has been substantial discussion and speculation over the years regarding the factors which influence the amount of genetic diversity carried in populations. As the examples cited here illustrate, different factors may very well be important in different species. In our opinion, attempting ideographic explanations for each species or population using the most thorough information available on life history parameters and historical demographics is probably the best way to ultimately arrive at possible generalizations.

## GENETIC VARIATION IN OTHER RHINOCEROS

In addition to *R. unicornis*, published estimates of genetic variability exist for 2 other of the 5 extant species of rhinoceros (Table 5). Using techniques similar to those of Dinerstein and McCracken (1990), Merenlender *et al.* (1989) reported much lower genetic diversity in black rhinoceros (*Diceros bicornis*;  $H_o = .013$ ,  $P = .065$ ) and in both recognized subspecies of white rhinoceros (*Ceratotherium simum simum*;  $H_o = .013$ ,  $P = .097$  and *C. s. cottoni*;  $H_o = .019$ ;  $P = .080$ ). Examination of mtDNA variation in 3 populations of *D. bicornis* (Ashley *et al.*, 1990) also revealed very little genetic variability in that taxa. A more recent examination of serum proteins (Stratil *et al.*, 1990) suggests the presence of higher variability in *C. s. cottoni* than reported by Merenlender *et al.* (1989); however, the techniques used in the two studies are not directly comparable. In any event, it seems evident that the variation carried in the Chitwan population of *R. unicornis* is much higher than that in either white or black rhinoceros. It also is significant that there appears to be little genetic differentiation among the different populations sampled for either species of African rhinoceros (Merenlender *et al.*, 1989; Ashley *et al.*, 1990).

The lineages leading to modern African and Asian rhinoceros diverged approximately 26 million years ago (Merenlender *et al.*, 1989). Because of their long histories as separate lineages, we may not obtain a satisfactory answer to the question of why Chitwan *R. unicornis* retain high genetic variability while both *C. simum* and *D. bicornis* are depauperate in variability. However, there are both similarities and differences among these species which may be relevant to this question. Like *R. unicornis* in southern Asia, the two African species were formerly widespread, and probably were abundant, over most of central and southern Africa (Western, 1987; Merenlender *et al.*, 1989). The southern white rhinoceros, *C. s. simum*, reached its nadir of less than 100 individuals in the 1920's, but by 1987 had recovered to an estimated population size of about 4,600. Several thousand northern white rhinoceros, *C. s. cottoni*, persisted until the 1960's, but since then their numbers have declined to a precarious low of only 18 individuals (Western, 1987). Populations of the black rhinoceros, *D. bicornis*, numbered in the 100,000's in the 1800's, and their total population was estimated to be about 60,000 in 1970. By 1987, only about 3,800 persisted in numerous isolated populations, the largest of which was estimated at about 250 (Western, 1987). The recency of the precipitous declines of both African species, coupled with their long generation times, leads us to believe that, like *R. unicornis*, sufficient time has not elapsed for major erosion of genetic diversity as a consequence of recent bottlenecks. If the observed depauperate variation were due to the effects of recent bottlenecks, we also would expect the development of genetic divergence among the isolates (McCommas and Bryant, 1990), but interpopulation divergence among rhinoceros populations has not been observed (Merenlender *et al.*, 1989; Ashley *et al.*, 1990). Therefore, we conclude that low genetic diversity in what remains of both African species probably reflects the existence of low diversity in both species prior to man's recent impacts.

There are differences in ecology and behavior among these rhinoceros species which are partially consistent with patterns of genetic diversity reported. Summarizing the social systems of all 3 species, Laurie (1982) notes that *R. unicornis* forms groups less frequently than white or black rhinoceros. The social system of *R. unicornis* is based on male dominance hierarchies, and individuals often move long distances. *R. unicornis* also occupies a diversity of habitats including swamps, grassland and riverine forest. In contrast, *C. simum* are restricted to short grasslands, and males maintain territories of .8 - 2.8km<sup>2</sup> which contain groups of females. These differences suggest that *R. unicornis* may maintain higher  $N_e$ 's and have higher rates of gene flow than *C. simum*. The differences between the social systems of *R. unicornis* and *D. bicornis* are not as striking (Laurie, 1982). *D. bicornis* also occupies a diversity of habitats ranging from semi-desert to montane forest. The social system of *D. bicornis* is flexible, resembling *C. simum*'s in dryer habitat, and *R. unicornis*' in wetter areas (Laurie, 1982). Therefore, while an argument may be made that, compared to *C. simum*, *R. unicornis* has characteristics which may result in populations carrying higher genetic variability, a similar argument for *R. unicornis* versus *D. bicornis* does not appear to hold.

Recently, Gilpin (1991, also see Pimm *et al.*, 1989) has proposed a model that could account for low genetic diversity within populations, and little genetic heterogeneity among populations, in organisms that are both abundant and widespread. The model supposes that the species population (metapopulation) is fragmented into local populations which are connected by limited gene flow. Local populations vary in size and go extinct independently of one another and, following extinctions, local populations are reestablished by a limited number of migrants from extant populations. Simulations show that under these conditions heterozygosity in the metapopulation decays rapidly, and that interpopulation heterogeneity also erodes. However, at any time, the metapopulation remains large.

Gilpin's (1991) model may account for patterns of genetic diversity observed in a large number of taxa. It has been specifically noted that species which inhabit boreal or arctic habitats generally show lower levels of variation than related species in temperate or tropical areas (Nevo *et al.*, 1984; Sage and Wolff, (1986). Sage and Wolff, 1986) have found that this pattern is robust for mammals, and have hypothesized that repeated range fragmentation resulting from glacial advances, followed by recolonizations during interglacial periods, may account for reduced genetic variability in arctic and boreal mammals. Glaciations may have reduced the size of metapopulations leading to lower  $N_e$ 's and a loss of diversity via classic bottleneck models (Chakraborty *et al.*, 1980; McCommas and Bryant, 1990). However, via the Gilpin model, habitat change resulting in fragmentation and extinctions of local populations also could result in the loss of diversity even if metapopulations remained very large.

The metapopulation model may also apply to African rhinoceros population structure over prehistoric and historic time. Fossils of both *C. simum* and *D. bicornis* are known from Africa in early Pleistocene deposits. It also is known that during the late Pliocene and early and late Pleistocene, Africa underwent periods of repeated and substantial climatic fluctuation (Kingdon, 1971; Hamilton, 1974; 1976). These climatic changes were largely a consequence of tectonic activity and do not correlate with northern glaciations; however, they did result in repeated and considerable contraction and expansion of climatically controlled vegetation zones. The generally high and complex topography of Africa also contributed substantially to the repeated fragmentation and coalescence of habitats (Kingdon, 1971; Hamilton, 1974; 1976). The impact of these events on the evolution and distributions of forest-dwelling mammals in Africa has received substantial attention (Kingdon, 1971; Hamilton, 1976; 1981), but effects on animals in more xeric habitats also have been documented (Kingdon, 1971). Because *C. simum* is restricted to short grass plains, we entertain the idea that repeated habitat fragmentation has resulted in low genetic diversity in this species. However, because of its more catholic choice of habitats, this model is, again, less plausible for *D. bicornis*. If it could be argued that *D. bicornis* was primarily a forest dwelling animal which has only subsequently expanded its range into xeric habitats, this model could hold for this species as well. However, we know of no evidence to support this supposition, and, in fact, fossils of *D. bicornis* are known from throughout the Pleistocene in sites that experienced substantial climatic change (Kingdon, 1971).

The dichotomy in the amount of genetic diversity carried in *R. unicornis* versus *C. simum* and *D. bicornis* could also be at least partially a result of how populations of these taxa have declined. The historic range of *R. unicornis* was fragmented over a period of several centuries by land clearing and agriculture. However, throughout this period, Chitwan Valley remained as a possible refuge of appropriate habitat and may have received migrants from areas outside of Chitwan where rhinoceros habitat was destroyed by man's activities. A malaria infested riverine system, left intact, might also have provided *R. unicornis* with a persistent travel corridor enhancing the influx of genetic material. If there were structuring among *R. unicornis* populations, migration into the Chitwan population would have increased the variation in it. Therefore, it is possible that the Chitwan population of *R. unicornis* currently carries levels of diversity that are larger than

was typical of populations prior to their decline. This is a possible partial explanation for why the Chitwan *R. unicornis* population has such high variation, but clearly not an explanation for why African rhinoceros have low genetic variability. However, as Western (1987) points out, the recent reductions in African rhinoceros have not been due primarily to habitat destruction; abundant acceptable rhinoceros habitat remains in Africa. Rather, African rhinoceros largely have been killed in place by intensive hunting. Therefore, migration into habitat refuges may have been less of an option for African than Indian rhinoceros. Migration into restricted local populations also has been offered as one explanation for the very high levels of genetic variation observed in some white-tailed deer populations (Table 2; Sheffield *et al.*, 1985).

## REFERENCES

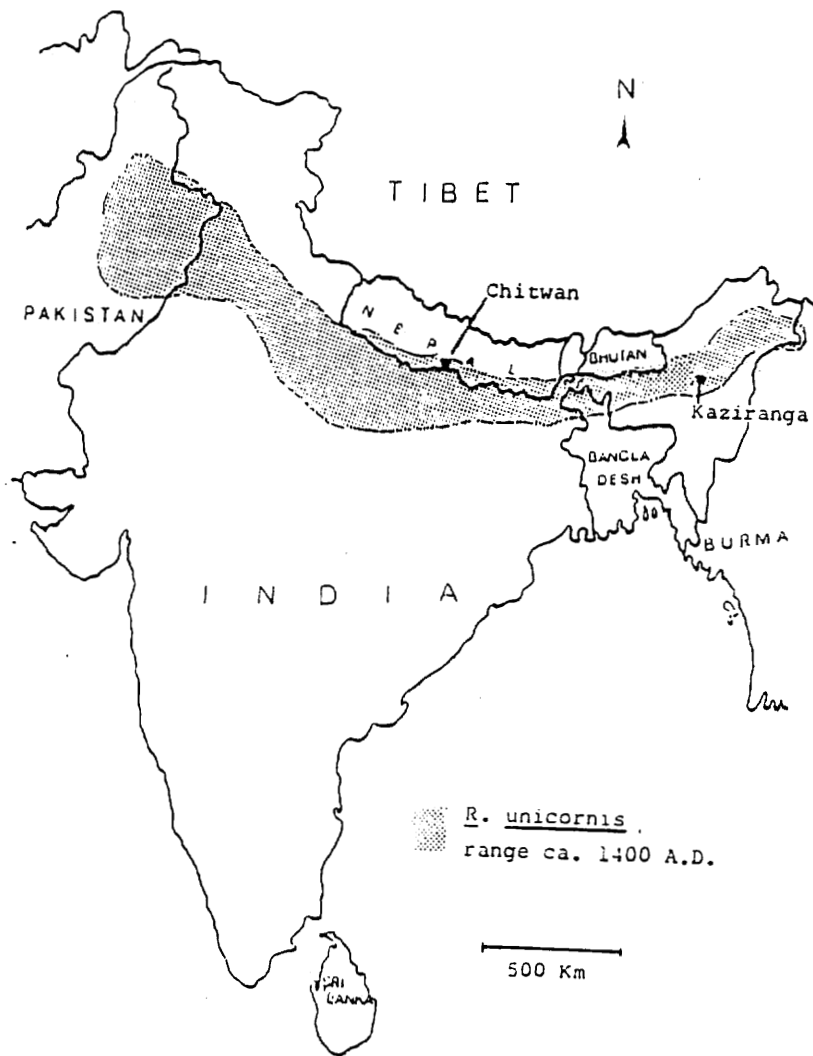
- Allendorf, F. W., F. B. Christiansen, T. Dobson, W. F. Eanes, and O. Frydenberg (1979) Electrophoretic variation in large mammals. I. The polar bear, *Thalarctos maritimus*. *Hereditas* 91:19-22.
- Allendorf, F. W. (1986) Genetic drift and loss of alleles versus heterozygosity. *Zoo Biology* 5:181-190.
- Ashley, M. V., D. J. Melnick, and D. Western (1990) Conservation genetics of the black rhinoceros (*Diceros bicornis*), I: Evidence from the mitochondrial DNA of three populations. *Cons. Biol.* 4:71-77.
- Baccus, R., N. Ryman, M. H. Smith, C. Reuterwall, and D. Cameron (1983) Genetic variability and differentiation of large grazing mammals. *J. Mamm.* 64:109-120.
- Bonnell, M. L. and R. K. Selander (1974) Elephant seals: Genetic variation and near extinction. *Science* 184:908-909.
- Chakraborty, R., P. A. Fuerst, and M. Nei (1980) Statistical studies on protein polymorphism in natural populations. III. Distribution of allele frequencies and the number of alleles per locus. *Genetics* 94:1039-1063.
- Dinerstein, E. and G. F. McCracken (1990) Endangered greater one-horned rhinoceros carry high levels of genetic variation. *Cons. Biol.* 4:338-343.
- Eisenberg, J. F. (1981) *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*. University of Chicago Press, Chicago, IL. p. 509.
- Gilpin, M. (1991) The genetic effective size of a metapopulation. *Biol. J. Linnean Soc.* 42:165-175.
- Hamilton, A. (1974) The history of the vegetation. (Pp 188-209) In: *East African Vegetation*. E. M. Lind and M. E. S. Morrison (eds.) Longman Group Limited, London, England.
- Hamilton, A. (1976) The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper pleistocene palaeoenvironments: A review. *Palaeocology of Africa* 9:63-96.
- Hamilton, A. C. (1981) The quaternary history of African forests: Its relevance to conservation. *Afr. J. Ecol.* 19:1-6.
- Kimura, M. (1983) *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge, England. p. 367.
- Kingdon, J. (1971) *East African Mammals: An Atlas of Evolution in Africa*. Academic Press, New York, NY. p. 446.
- Lande, R. (1988) Genetic and demography in biological conservation. *Science* 241:1455-1460.
- Lande, R. and G. F. Barrowclough (1987) Effective population size, genetic variation, and their use in population management. (Pp 87-123) In: *Viable Populations for Conservation*. M. E. Soule (ed.) Cambridge University Press, Cambridge, England.
- Laurie, A. (1982) Behavioural ecology of the greater one-horned rhinoceros (*Rhinoceros unicornis*). *J. Zool. Lond.* 196:307-341.
- Manlove, M. N., R. Baccus, M. R. Pelton, M. H. Smith, and D. Graber (1980) Biochemical variation in the black bear. (Pp 31-41) In: *Bears - Their Biology and Management*. C. J. Martinka and K. L. McArthur (eds.) Bear Biol. Assoc. Conf., U. S. Government Printing Office, Washington, DC.
- McClenaghan, Jr. L. R. and T. J. O'Shea (1988) Genetic variability in the Florida manatee (*Trichechus manatus*). *J. Mamm.* 69:481-488.

- McCommas, S. A. and E. H. Bryant (1990) Loss of electrophoretic variation in serially bottlenecked populations. *Hereditas* 64:315-321.
- McDermid, E. M., R. Ananthakrishnan, and N. S. Agar (1972) Electrophoretic investigation of plasma and red cell proteins and enzymes of Macquarie Island elephant seals. *Anim. Blood Grps. Biochem. Genet.* 3:85-94.
- Merenlender, A. M., D. S. Woodruff, O. A. Ryder, R. Kock, and J. Vahala (1989) Allozyme variation and differentiation in African and Indian rhinoceroses. *J. Heredity* 80:377-382.
- Nei, M., T. Maruyama, and R. Chakraborty (1975) The bottleneck effect and genetic variability in populations. *Evolution* 29:1-10.
- Nevo, E. (1978) Genetic variation in natural populations: Patterns and theory. *Theor. Pop. Biol.* 13:121-177.
- Nevo, E., A. Beiles, and R. Ben Shlomo (1984) The evolutionary significance of genetic diversity: Ecological, demographic, and life history correlates. (Pp 13-213) In: *Lecture Notes in Biomathematics*. Vol. 53. G. S. Mani (ed.) Springer-Verlag, Berlin.
- O'Brien, S. J., D. E. Wildt, C. R. Merrill, M. Bush (1983) The cheetah is depauperate in genetic variation. *Science* 221:459-462.
- O'Brien, S. J., D. E. Wildt, M. Bush, T. M. Caro, C. FitzGibbon, I. Aggundey, and R. E. Leakey (1987) East African cheetahs: Evidence for two population bottlenecks? *Proc. Natl. Acad. Sci.* 84:508-511.
- O'Brien, S. J. and J. F. Evermann (1989) Interactive influence of infectious disease and genetic diversity in natural populations. *Trends Ecol. Evol.* 3:254-259.
- Pemberton, J. M. and R. H. Smith (1985) Lack of biochemical polymorphism in British fallow deer. *Hereditas* 55:199-207.
- Pimm, S. L., J. L. Gittleman, and G. F. McCracken (1989) Plausible alternatives to bottlenecks to explain reduced genetic diversity. *Trends Ecol. Evol.* :176-178.
- Powell, J. R. (1975) Protein variation in natural populations of animals. *Evol. Biol.* 8:79-119.
- Price, P.K., M. Cartwright, and M.J. Rogers (1979) Genic variation in white-tailed deer from Arkansas. *Proc. Arkansas Acad. Sci.* 33:64-66.
- Ramsey, P. R., J. C. Avise, M. H. Smith, D. F. Urbston (1979) Biochemical variation and genetic heterogeneity in South Carolina deer populations. *J. Wildl. Manage.* 43:136-142.
- Sage, R. D. and J. O. Wolff (1986) Pleistocene glaciations, fluctuating ranges, and low genetic variability in a large mammal (*Ovis dalli*). *Evolution* 40:1092-1095
- Selander, R. K. (1976) Genic variation in natural populations. (Pp 21-45) In: *Molecular Evolution*. F. J. Ayala (ed.) Sinauer Assoc., Sunderland, MA.
- Selander, R. K. and D. W. Kaufman (1973) Genic variability and strategies of adaptation in animals. *Proc. Nat. Acad. Sci.* 70:1875-1877.
- Sheffield, S. R., R. P. Morgan II, G. A. Feldhamer, and D. M. Harman. (1985) Genetic variation in white-tailed deer (*Odocoileus virginianus*) populations in western Maryland. *J. Mamm.* 66:243-255.
- Simon, C. and J. Archie (1985) An empirical demonstration of the lability of heterozygosity estimates. *Evolution* 39:463-467.
- Simonsen, V. (1982) Electrophoretic variation in large mammals. II. The red fox, *Vulpes vulpus*, the stoat, *Mustela erminea*, the weasel, *Mustela nivalis*, the pole cat, *Mustela putorius*, the pine marten, *Martes martes*, the beech marten, *Martes foina*, and the badger, *Meles meles*. *Hereditas* 96:299-305.
- Simonsen, V., F. W. Allendorf, W. F. Eanes, and F. O. Kapel (1982a) Electrophoretic variation in large mammals. III. The ringed seal, *Pusa hispida*, the harp seal, *Pagophilus groenlandicus*, and the hooded seal, *Cystophora cristata*. *Hereditas* 97:87-90.
- Simonsen, V., E. W. Born, and T. Kristensen (1982b) Electrophoretic variation in large mammals. IV. The Atlantic walrus, *Odobenus rosmarus rosmarus* (L.). *Hereditas* 97:91-94.
- Smith, M.H., R. Baccus, H.O. Hildestad, and M.N. Manlove (1984) Population genetics of the white-tailed deer. (Pp. 365-387) In *White-tailed deer: ecology and management*. L.K. Hall (ed.) Stackpole Books, Harrisburg, PA.

- Smith, M. H., W. V. Branan, R. L. Marchinton, P. E. Johns, and M. C. Wooten. (1986) Genetic and morphologic comparisons of red brocket, brown brocket, and white-tailed deer. *J. Mamm.* 67:103-111.
- Soule, M. (1976) Allozyme variation: Its determinants in space and time. (Pp 60-77) In: *Molecular Evolution*. F. J. Ayala (ed.) Sinauer Assoc., Sunderland, MA.
- Stratil, A., P. Bobak, P. Kalab, D. Cizova, R. Pokorny (1990) Serum proteins of rhinoceroses: Inter- and intra-specific variation. *Comp. Biochem. Physiol.* 95B:803-810.
- Testa, J. W. (1986) Electromorph variation in Weddell seals (*Leptonychotes weddelli*). *J. Mamm.* 67:606-610.
- Wada, S. (1983) Genetic structure and taxonomic status of minke whales in the coastal waters of Japan. *Rept. Internat. Whaling Comm.* 33:361-363.
- Western, D. (1987) Africa's elephants and rhinos: Flagships in crisis. *Trends Ecol. Evol.* 2:343-346.
- Winans, G. A. and L. L. Jones (1988) Electrophoretic variability in Dall's porpoise (*Phocoenodides dalli*) in the North Pacific Ocean and Bering Sea. *J. Mamm.* 69:14-21.
- Wooten, M. C. and M. H. Smith (1985) Large mammals are genetically less variable? *Evolution* 39:210-212.



Figure 1. Geographic range of *R. unicornis* in ca. 1400 A.D. The locations of Royal Chitwan and Kaziranga National Parks are indicated.



From: Dinerstein and McCracken 1990

TABLE 1. SURVEYS OF AVERAGE HETEROZYGOSITY IN MAMMALS

Heterozygosity ( $H_e$ )	# Species Examined	Source
.055	16	Selander & Kaufman 1973
.039	25	Powell 1975
.052	30	Selander 1976
.036	46	Nevo 1978
.033	53	Baccus et al. 1983
.041	184	Nevo et al. 1984
.039	138	Wooten & Smith 1985

TABLE 2. ESTIMATES OF HETEROZYGOSITY IN DIFFERENT LOCAL POPULATIONS OF WHITE-TAILED DEER

LOCATION	H <sub>o</sub>	Source
Georgia	.056	Smith et al. 1984
South Carolina	.092	Smith et al. 1984
Arkansas	.023	Pree et al. 1979
Maryland	.059	Sheffield et al. 1985
Maryland	.104	Sheffield et al. 1985

TABLE 3. ESTIMATES OF HETEROZYGOSITY IN SELECTED POPULATIONS OF LARGE MAMMALS WITH HIGH LEVELS OF H<sub>o</sub>

TAXON	H <sub>o</sub>	Source
White-tailed Deer ( <i>Odocoileus virginianus</i> )	.127	Ramsey et al. 1979
Mink Whale ( <i>Balaenoptera acutorostrata</i> )	.121	Wada 1983
Dall's Porpoise ( <i>Phocoenoides dalli</i> )	.058	Winans & Jones 1988
Florida Manatee ( <i>Trichechus manatus</i> )	.063	McClenaghan & O'Shea 1988

TABLE 4. ESTIMATES OF HETEROZYGOSITY IN SELECTED POPULATIONS OF LARGE MAMMALS WITH LOW LEVELS OF H<sub>o</sub>

TAXON	H <sub>o</sub>	Source
Fallow Deer ( <i>Dama dama</i> )	0	Pemberton & Smith 1985
Weddell Seal ( <i>Leptonychotes weddellii</i> )	.023	Tysia 1986
Southern Elephant Seal ( <i>Mitrounka leonina</i> )	.028	McDermid et al. 1972
Walrus ( <i>Odobenus rosmarus</i> )	.033	Simonsen et al. 1982

TABLE 5. ESTIMATES OF GENETIC VARIATIONS IN 3 SPECIES OF RHINOCEROS

TAXON	H <sub>o</sub>	P	# Locl	# Individuals Examined
<i>C. s. sirtum</i>	.013	.097	31	231
<i>C. s. cottoni</i>	.019	.080	25	71
<i>D. bicornis</i>	.013	.065	31	91
<i>R. unicornis</i>	0	0	31	31
<i>R. unicornis</i>	.039	.310	29	232

<sup>1</sup> Merenlender et al. 1989. J. Heredity 80:377-382.

<sup>2</sup> Dinershteyn & McCracken 1990. Cons. Biology 4:417-422.