Understanding the multiple meanings of 'inbreeding' and 'effective size' for genetic management of African rhinoceros populations

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Abstract

Although some African rhinoceros populations are currently increasing, others are critically endangered. Even healthy populations are extensively managed in the wild and in captivity. While political and demographic considerations are of primary concern, many decisions are made in the name of genetic management. Such decisions should be informed by a full understanding of the multiple meanings of inbreeding and effective population size. In this essay, we examine inbreeding and effective size of wild and captive populations of African rhinoceroses. We conclude by showing how misunderstanding of effective size and Franklin's 50/500 rule can make a crucial difference in informing management decisions.

Key words: effective size, genetic management, inbreeding, rhinoceros

Résumé

Bien que certaines populations de rhinocéros africains soient actuellement en augmentation, d'autres sont en danger critique. Même les populations saines sont gérées très activement dans la nature et en captivité. Alors que les considérations politiques et démographiques soient les principaux motifs d'inquiétude, de nombreuses décisions sont prises au nom de la gestion génétique. Ces décisions devraient se faire en pleine connaissance des multiples implications de l'inbreeding et de ce qu'est une taille de population nécessaire. Dans cet essai, nous examinons l'inbreeding et la taille nécessaire des populations sauvages et captives de rhinocéros africains. Nous concluons en montrant comment une mauvaise compréhension de la taille nécessaire et de la règle 50/500 de Franklin peut entraîner une différence cruciale lorsqu'il s'agit de prendre, en connaissance de cause, les décisions opportunes.

Introduction

Species survival plans (SSPs) coordinate management of rare and endangered species to maintain healthy breeding populations, retain genetic variation and minimize 'inbreeding'. SSPs often have the conflicting goals of preserving species in a captive environment while at the same time minimizing evolutionary change in the species and minimizing loss of genetic diversity from 'inbreeding' or drift (Templeton, 1991a,b). These can be significant forces affecting *in situ* and captive populations that are entering or emerging from population bottlenecks. The captive population of Speke's gazelle, *Gazella spekei,* and *in situ* populations of southern white rhinoceros, *Ceratotherium simum simum*, have weathered such bottlenecks in recent times (Templeton & Read, 1984; Roomaaker, 2002). However, black rhinoceros, *Diceros bicornis*, and northern white rhinoceros, *Ceratotherium simum cottoni*, populations are currently entering bottlenecks. With the refusal of the Congolese government to allow the airlift of the last few northern white rhinoceroses from Garamba reserve in 2006, this bottleneck may in fact have already become the end of an extinction vortex for the northern white rhinoceros.

To fully appreciate the consequences of this situation, we will first review the multiple meanings of the term 'inbreeding' and examine the available data on inbreeding and inbreeding depression in captive African rhinoceros populations. Next, we will review the various meanings of the term 'population effective size' and how these terms reflect very different aspects of populations of African rhinoceros. Finally, we will examine Franklin's 50/500 rule

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and how confusing the various effective sizes can have catastrophic consequences for management decisions.

Inbreeding in captive and wild populations of African rhinoceroses

Inbreeding is a primary concern in captive breeding and wild translocation programmes for African rhinoceroses. Unfortunately, while we may think we mean the same thing when we use the word 'inbreeding' there are multiple biological meanings and various algorithms for estimating the very different phenomena. Understanding these differences is obvious if we realize that inbred individuals are the ones, which suffer inbreeding depression while an inbred population is the level at which genetic variation is lost.

Multiple meanings of 'inbreeding'

Templeton & Read (1984) attempted to clarify three of the most frequently cited meanings of inbreeding: inbreeding as a measure of shared ancestry (F), inbreeding as a measure of genetic drift ($\bar{F}$) and inbreeding as a measure of the system of mating (f). Inbreeding as a measure of shared ancestry (F) is a characteristic of individuals, not populations. While it may indicate risk of inbreeding depression and disease, it can neither measure genetic diversity nor can it tell us if there is avoidance of inbreeding because the F values can only be greater or equal to zero. While inbreeding as a measure of drift ($\bar{F}$) is a population parameter and can inform us about the loss of genetic variation or accumulation of homozygosity in a population, it cannot measure avoidance of inbreeding because $\bar{F}$ values can only be greater or equal to zero. Inbreeding as a measure of the system of mating (f) is an index of deviation from random mating, and can be greater or less than zero. Therefore it can measure avoidance of inbreeding, but f cannot measure genetic diversity in the population or inform us about an individual. Although $\bar{F}$ and f measure different population attributes, they can be intertwined evolutionarily (Braude, 2000; O'Riain & Braude, 2001). For example, Lacey (2001) and Lacey & Weiczorek (2004) found moderate pedigree inbreeding (F) and inbreeding in the drift sense ($\bar{F}$) in the same populations of colonial Tuco-tucos that had avoidance of inbreeding as the system of mating (f). In the case of the captive population of Speke's gazelle, pedigree inbreeding of individuals in the population (F) could not be avoided because of the small number of founders (Templeton & Read, 1998). On the other hand, the management plan for the Speke's gazelle reduced the impact of deme level drift ($\bar{F}$) by imposing outbreeding (or avoidance of inbreeding, i.e. $f < 0$) as the system of mating.

Even once we are clear about the type of inbreeding we are interested in, confusion continues because we use 'the F statistic' from population genetics to estimate inbreeding in the drift sense. Population structure can be quantified by a series of hierarchical F statistics that describe the genetic similarity within and between groups. It is essential to be clear about the particular F statistic under consideration, whether F_{ST}, F_{IT}, F_{IS}, F_{LS}, F_{IL}, etc., when discussing levels of population structure and the biological level (deme, collection of demes, etc) being measured (Jacquard, 1975; Braude, 2007). Therefore, if we read that a population is likely to suffer from 'inbreeding' because its 'F statistic' is high, we need to ask 'what type of inbreeding and which F statistic are the authors using?'

The captive populations of African rhinoceros clearly illustrate these differences. While 54% (510 of 948) of the captive African rhinoceros population was born in captivity (as of 1999), only 3% (17) of these captive born animals have any degree of pedigree inbreeding ($F > 0$) (International studbook for African Rhinoceros, 1999) (Table 1). This results from careful management of breeding in these populations along with the relatively large founder populations for both black rhinoceros subspecies and the southern white rhinoceros. Although there

Subspecies	Total captive population	Captive born	Animals with $F > 0$	$\bar{F}$ for the captive population
Diceros b. michaeli	170	139	7	0.0099
D. b. minor	65	30	0	0
Ceratotherium simum cottoni	9	4	0	0
Ceratotherium simum simum	704	337	10	0.0052

Table 1 Pedigree inbreeding (F) and inbreeding as a measure of drift ($\bar{F}$) in the captive populations of African rhinoceros (International studbook for African Rhinoceros, 1999)

Table 2 Inbreeding depression in the captive populations of African rhinoceros (International studbook for African Rhinoceros, 1999)

Subspecies	Total births 1997–1999	Animals with $F = 0$		Animals with $F > 0$	
		Survival >1 year	Survival <1 year	Survival >1 year	Survival <1 year
Diceros b. michaeli	27	17	7 (29)	1	2 (66)
D. b. minor	13	13	0	0	0
Ceratotherium simum cottoni	0	–	–	–	–
Ceratotherium simum simum	40	34	6 (15)	0	0

Values in parentheses are percentages.

are more pedigree inbred individuals in the two subspecies with the largest captive populations, the degree of inbreeding in the drift sense for these populations is still extremely low (International studbook for African Rhinoceros, 1999) (Table 1). The lack of either pedigree inbreeding or inbreeding in the drift sense in the northern white rhinoceros might appear surprising considering the small size of the founder population. However, this results from the fact that there has been only one generation born in captivity. Unfortunately, this captive population contains only one male. The four founding females are nearing the end of their reproductive lives, and all the captive born animals are full sisters. If fertility in this population could be improved, there would be a need for careful genetic management to minimize the loss of genetic variation because of the drift induced by the small founder size and the lessons of the Speke's gazelle captive breeding programme would be directly applicable.

Like the captive population of northern white rhinoceroses, the captive population of Speke's gazelle was founded by a very small number of individuals; one male and three females (Templeton & Read, 1984). The Speke's gazelle breeding programme was designed with an understanding of fundamental population genetics. The programme accepts the limitations of managing a small captive population derived from a small number of founders, but maximizes the genetic diversity preserved in the population and minimizes inbreeding depression by recognizing that: (i) small founder populations can carry a large proportion of the genetic diversity of the source population, (ii) rapidly increasing the size of the captive population can reduce drift and preserve diversity, (iii) equalizing the genetic representation of the founders in their descendants in the captive population maximizes genetic diversity, (iv) increasing the diversity of founder ancestry in individuals increases genetic diversity through recombination and (v) subdivision of the captive population, once it has reached carrying capacity, will reduce extinction of alleles because of drift. The programme has been extremely successful in reducing inbreeding depression while preserving genetic variation (Templeton & Read, 1984, 1998; Templeton, 2002) and will be invaluable in informing a breeding programme for the northern white rhinoceros if more immediate problems of breeding physiology can be overcome or if animals from Garamba can be integrated into the breeding programme. The importance of rapidly increasing the population size has already been recognized in the management plan for Eastern black rhinoceros in Kenya (Amin *et al.*, 2006).

Avoidance of inbreeding depression is one of the primary reasons for avoiding pedigree inbreeding in managed captive populations. While management for African rhinoceros species has reduced the number of matings between individuals of known relatedness, three of the 27 eastern black rhinoceroses born in captivity between 1997 and 1999 were pedigree inbred (Table 2; International studbook for African Rhinoceros, 1999). Two of these calves died before reaching 1 year. Compared to the background rate of calf mortality in captivity (29%), this could be an indication that inbreeding depression is a legitimate concern in managing this species but the sample size is extremely small ($P = 0.2503$, FET). In contrast, Zschokke & Baur (2002) found no increased juvenile mortality in pedigree inbred *Rhinoceros unicornis*, but this species has come through a recent population bottleneck that may have purged deleterious recessive alleles from the population or been selected for combinations of genes that do well under inbreeding (Templeton, 2002).

Outbreeding and outbreeding depression in African rhinoceroses

While pedigree inbreeding and inbreeding depression appear to be a minor concern for conservation of captive African black rhinoceros populations, outbreeding depression may be a serious problem for management of wild *in situ* populations. Templeton (1987) argued that the inbreeding depression typically reported for captive populations in zoos is evidence that wild populations are typically outbred because populations with a history of inbreeding tend to suffer most from inbreeding depression. Ralls, Ballou & Templeton (1988) found high levels of inbreeding depression in an analysis of forty captive populations of various sized mammals. Although we might expect natural populations of small sized mammals to have a genetic architecture adapted to subdivision, large mammals typically range over large areas and we expect them to have a genetic architecture adapted to panmictic structure. Often the extreme genetic fragmentation observed today is a result of very recent anthropogenic habitat disturbance. However, if a population is normally subdivided and the founders of a captive population are sampled across demes, then the lack of viability seen in the captive population might be because of outbreeding depression and this would be confused with inbreeding depression in small zoo populations (Templeton, 1987). Although O'Ryan, Flamand & Harley (1994) argued that outbreeding depression is not likely to be a problem for African rhinoceros populations, it has been described in captive Indian rhinoceros populations (Zschokke & Baur, 2002) and we should not discount it.

Although African rhinoceros populations are currently fragmented, they have historically been large and panmictic across areas as large as many of the range states in which they currently exist. However, translocations of wild rhinoceroses over greater distances could cause loss of variation and genotypic extinction as a result of hybridization (Templeton, 1991a,b). There is a long history of translocation with little concern for the genetic consequences going back as far as the 1960s when black rhinoceroses were translocated from the Kitui area of Kenya to Addo Park in South Africa. The descendants of these animals were later translocated to Mkomazi and Ngorogoro in Tanzania (Mccabe, 2001). Swart & Ferguson (1996) have addressed this issue in black rhinoceros conservation and noted that, 'It may not always be advisable to translocate individuals between distinct populations because this could lead to the break-up of genetic combinations that reflect local adaptations of each remaining population' (p. 79). '*D. b. bicornis* is found in arid south-western Africa, whereas *D. b. minor* roams the moister, eastern parts of the continent.' (p. 80). However, major translocations have been suggested for wild populations by Emslie & Brooks (1999). This results from the fact that anthropogenic threats to individuals or small populations are far more immediate concerns in many of the range states. In addition, demographic threats to populations that have fallen below the threshold size for males and females to find each other, represents an additional immediate threat.

When translocation decisions are not dictated by immediate crisis and can incorporate genetic concerns, the successful reintroduction of collared lizards in southern Missouri provides a well studied model system for the effect of population structure on successful translocation and reintroduction (Templeton *et al.*, 2001). Local populations of collared lizards in the Ozarks are found in glades, which are open rocky barrens with hot, dry microclimate. Genetic surveys revealed that glade populations were isolated and there was very low variation within glades (low heterozygosity). However, drift has fixed different alleles in different populations, so that regionally there was significant genetic diversity remaining. Optimal reintroduction would then suggest taking all the individuals to be translocated from only one glade to recolonize each new glade to avoid outbreeding depression. However, existing populations were too small to provide more than two animals for translocation. Hence, mixed introduced populations were required. Also, the extreme fragmentation of the lizard population was a recent one, induced by the suppression of forest fires, with the lizard populations still sharing the genetic signature of past genetic interchange. Hence, a mixed translocation was implemented and it has been highly successful. This situation is very similar to the restrictions on African rhinoceros reintroductions. Two relevant lessons from the collared lizard reintroduction are that:

1 We will be most successful if we can start new populations by taking a random assortment of animals from a single existing healthy population, whether the source has high or low heterozygosity. (Mixing will be less of a problem if different source populations are part of a large metapopulation that is only recently subdivided. However, if subdivision is longer standing, then mixing is more likely to result in outbreeding depression.)

2 The majority of outbreeding depression is suffered in F_2 and backcross generations. If the populations can get through this fitness bottleneck, the resulting populations should display a fitness rebound, sometimes being as, or more, viable than the original populations (Templeton *et al.*, 1990).

In both black rhinoceros and collared lizards, the breeding system usually consists of a single male dominating matings. Hence, it is best to establish new populations with single (or few) male(s) and multiple females from the source population. The skewed sex ratio of founders may make it easier to obtain all of the animals from one source population and may also enhance the initial rate of population growth. In rhinoceros, however, the more immediate reason for founding populations with few males is that multiple males in a territory can become so aggressive that they are likely to injure or kill females and young.

International Union for Conservation and Nature's (IUCN) African Rhinoceros Action Plan (Emslie & Brooks, 1999) identifies outbreeding depression as a possible problem in managing the current populations. However, it then goes on to recommend that 'rhinos selected for new populations should have as little genetic similarity with the recovering population as possible. Animals should be taken from different original genetic sources.' (p. 65). They further recommend the establishment of 'new populations using founder rhinoceros from a combination of original genetic sources of the same subspecies.' (p. 65) and that one new breeding individual be added to each population per generation. These recommendations are based on the generic philosophy of maximizing genetic diversity within breeding populations, without considering the genetic structure to which the current rhinoceros populations have adapted. If these populations were able to increase rapidly, this might be a more reasonable recommendation than in species with such a low intrinsic rate of increase.

The report identifies 248 discrete white rhinoceros populations and 83 discrete black rhinoceros populations, but they are treated as six metapopulations (for the six subspecies of the two species) (Emslie & Brooks, 1999). Animals are darted and translocated to increase genetic diversity in the various discrete populations without knowing whether local populations are locally adapted or whether they are disrupting coadapted gene complexes and thus fostering outbreeding depression. We recognize that human threats often require immediate action to save individuals from disease, poaching or encroachment. However, an immediate genetic survey and historical analysis of existing populations would help guide management decisions and avoid translocations that would be detrimental to long-term survival of these species (Templeton & Georgiatis, 1996).

Effective sizes of wild African rhinoceros populations

Population viability analyses attempt to model the impact of demographic, environmental and genetic stochasticity on populations of varying size and composition (e.g. Burgman, Ferson & Akcakaya, 1993). While Lande (1988) argued that demographic stochasticity has a far greater impact on the fate of wild populations, genetic considerations are crucial in managing small populations and effective size helps us estimate the impact of various population genetic effects on a population. Franklin's 50/500 rule (or Lande's later 500/5000 rule) is frequently referred to in management plans for *in situ* populations (Franklin, 1980; Lande, 1988). Although census numbers are typically applied to the 50/500 rule, Franklin based the rule on the inbreeding effective size and the variance effective size of a population.

Misunderstanding the concept of effective population size and Franklin's (1980) application of it can have catastrophic consequences for wildlife populations when these terms are misused to justify management decisions. A tragic example of this was the conclusion by Walpole *et al.* (2001) that 'If the population (of northern white rhinoceros) is isolated, at its present size (23) it is below estimates of minimum effective population size (Franklin, 1980)'. This condemnation of the Garamba rhinoceros population not only confused census size with effective size, it missed the fact that the inbreeding effective size of that population was actually greater than 50 animals!

The decline in African rhinoceros populations over the past century has been well documented (Braude, 1992; Emslie & Brooks, 1999). However, the data and policy goals typically address current population census sizes rather than effective population sizes. Current census population sizes are relevant when demographic stochasticity is significant in the survival of a population. On the other hand, effective sizes inform us about the genetic health of a population.

As with inbreeding, there are a variety of population effective sizes that each have different mathematical and biological meanings. The terms are often confused or treated as synonymous. Such confusion can have serious implications for understanding and managing populations of endangered or threatened species (e.g. Walpole *et al.*, 2001). The African rhinoceros populations discussed below illustrate these differences.

Inbreeding effective size, N_{ef}, refers to the size of an ideal population that would allow the same accumulation of pedigree inbreeding (genes identical by descent) because of the drift (sampling) in a single, randomly mating, isolated population. Calculation of N_{ef} ideally requires pedigree data. However, when we have historical census data it can be estimated by the formula

$$N_{\mathrm{ef}} \approx \frac{t}{\frac{1}{N(0)} + \frac{1}{N(1)} + \cdots + \frac{1}{N(t-1)}}$$

under certain restrictive assumptions. This Ne gives us an indication of the accumulation of alleles that are identical by descent. $N(0)$ refers to the size of the founder population and $N(t-1)$ is not the size of the population now, but the size one generation ago.

Inbreeding effective size can also be estimated from heterozygosity data. Harley *et al.* (2005) used expected heterozygosity to estimate black rhinoceros inbreeding effective sizes for the three common subspecies. Their estimates of inbreeding effective size are also considerably higher than the census sizes.

Variance effective size, N_{ev}, indicates how rapidly allele frequencies are likely to change and how rapidly isolated populations diverge from one another under genetic drift. It can also be estimated from historical census data with the formula

$$N_{\mathrm{ev}} \approx \frac{t}{\frac{1}{N(1)} + \frac{1}{N(2)} + \cdots + \frac{1}{N(t)}}$$

$N(1)$ refers to the size of the first generation after the founder population and $N(t)$ is the current population size. While the inbreeding effective size is more sensitive to the number of founders [$N(0)$], the variance effective size is more sensitive to the current population size. This N_e gives an indication of the increase in variance between subpopulations due to drift. It reflects change in allele frequencies.

Eigenvalue effective size, $N_{e\lambda}$, reflects genetic diversity in the population. It measures the rate at which alleles are lost (or alternate alleles are fixed) and can be estimated from the percentage of polymorphic loci present (Crow, 1954). $N_{e\lambda}$ is perhaps the most directly relevant effective size for decisions about conservation of genetic biodiversity. However, estimation of $N_{e\lambda}$, requires sampling of genotypes across a population over time. With the increasing use of genetic sampling, such data may soon become available for all rhinoceros populations (Florescu *et al.*, 2003; Scott *et al.*, 2004; Harley *et al.*, 2005).

In addition to the effective sizes discussed above, the following correction can be used at each generation if operational sex ratios are not 1 : 1.

$$Ne \approx \frac{4N_m N_f}{N_m + N_f}$$

This sex-ratio correction may be especially useful in demographic projections, but it is often misleadingly called 'the' effective size and used to infer population genetic structure (Anthony & Blumstein, 2000). For example, Halbert *et al.* (2004) used the sex ratio and fecundity corrections instead of inbreeding effective size to conclude that the effective size of the Texas bison herd is 'substantially lower than the recommended short term minimum of 50' (p. 928).

Understanding these different effective sizes can help us see the differences between African rhinoceros populations with different histories. Growing populations have a larger N_{ev} than N_{ef}, while declining populations will have larger N_{ef} than N_{ev}. Hence, a population coming through a bottleneck may have a low inbreeding effective size, but it can have a larger variance effective size if the population bounces back rapidly as is the case with the southern white rhinoceros population discussed in the next section. In contrast, a population that is still in decline will tend to have a larger inbreeding effective size than variance effective size. Indeed, frequently the inbreeding effective size can be orders of magnitude larger than the census size for species undergoing a rapid decline. For example, Harley *et al.* (2005) showed that the critically endangered black rhinoceros subspecies *Diceros b. michaeli* has been reduced to about 520 animals, but their estimate of the inbreeding effective size for this same subspecies under a mutational model appropriate for microsatellites is 5173, an order of magnitude larger than the census size. The '50' in the 50/500 rule refers to an inbreeding effective size, so in declining species the '50' portion will often be satisfied for census numbers far lower than 50 individuals.

The successful recovery of the southern white rhinoceros has led to large census size for this species. However the fact that the population is emerging from a severe bottleneck a century ago (Fig. 1) results in extremely low inbreeding effective size and variance effective size for the subspecies as estimated by the equations discussed earlier (Table 3). Although there is debate on the precise size of the population at the turn of the century (Emslie & Brooks, 2002; Roomaaker, 2002), the population was extremely small and has increased by nearly two orders of magnitude. On the other hand, although the northern white rhinoceros population may be smaller than 20 animals, the inbreeding effective size of the population was greater than this census size only a few years ago. Similarly, black rhinoceros populations have a far greater inbreeding effective size than their census size (Table 3). The fact that the inbreeding effective sizes are also larger than the

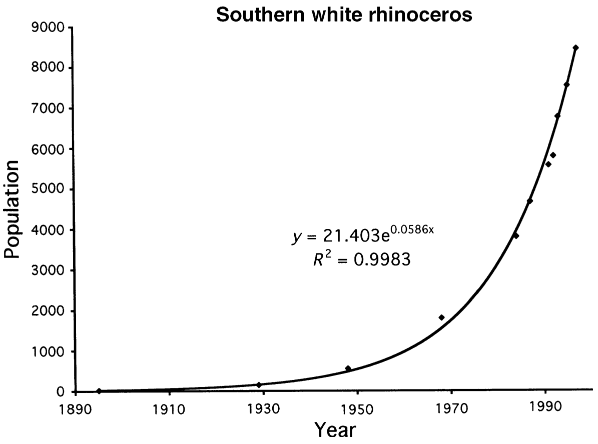

Fig 1 The southern white rhinoceros has recovered from near extinction at the turn of the last century and the current growing population is descended from a bottleneck population of only 20 animals (source data Emslie & Brooks, 1999)

variance effective size illustrates the difference in the forces indicated by these two effective sizes. The large inbreeding effective size results from the large ancestral population only a few generations ago. These species are entering population bottlenecks (Fig. 2). The variance effective size is not as large because it includes the accumulation of drift in the current population.

An additional question for which effective population size is relevant is the taxonomic status of the northern white rhinoceros. Northern and southern white rhinoceros are treated as separate subspecies because there is greater genetic variation between the two populations than has been found between the four subspecies of black rhinoceros. However, current sampling of white rhinoceroses represents populations that are in the midst of, and the result of, severe population bottlenecks. Hence, the reported differences in neutral alleles between the two populations would not be surprising for small isolated populations of a single species. A stronger argument for subspecies status for the two populations could certainly be made based on morphological, behavioural and ecological differences.

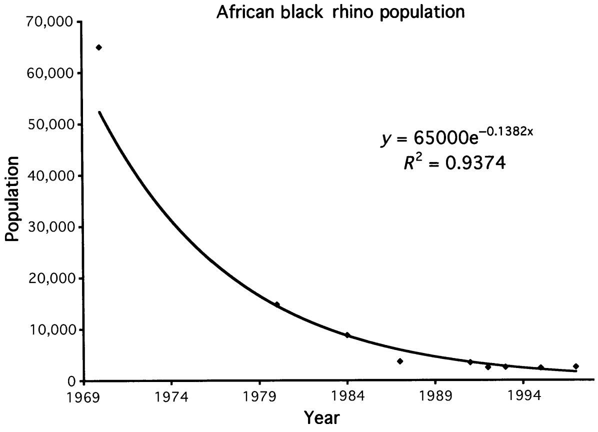

Fig 2 The black rhinoceros has been in severe decline in recent years and is entering a population bottleneck (source data Emslie & Brooks, 1999)

Integrating inbreeding and effective size

As illustrated by the above discussion, each effective size measures a different aspect of the genetic health of a population and these differences are related to the different meanings of inbreeding. Populations with low inbreeding effective size accumulate pedigree inbreeding. Populations with low variance effective size will experience change in allele frequencies. Populations with low eigenvalue effective size will lose polymorphism and this typically entails loss of heterozygosity and change in allele frequencies. Although the eigenvalue and variance effective sizes tend to be similar, the inbreeding effective size can be very different from the other two under realistic biological conditions (such as a rapid increase or decrease in population size).

When a species becomes fragmented into completely isolated subpopulations, in captivity or *in situ*, the

Table 3 Estimated wild African rhinoceros effective population sizes (based on census data reported in Emslie & Brooks, 1999 and population sizes extrapolated from Figs 1 and 2)

	Census size, 1997	Inbreeding effective size	Variance effective size
Black rhinoceros *Diceros bicornis*	$N = 2600$	$N_{ef} = 18{,}840$	$N_{ev} = 4189$
Southern white rhinoceros *Ceratotherium simum simum*	$N = 8440$	$N_{ef} = 106$	$N_{ev} = 240$
Northern white rhinoceros *Ceratotherium simum cottoni*	$N = 23$	$N_{ef} = 69$	$N_{ev} = 41$

inbreeding effective size for the total population decreases while the variance and eigenvalue effective sizes for the total population increase (Templeton, 2006). Pedigree inbreeding will accumulate at a rate determined by the population sizes within the fragments, not the total species population size.

The opposing effects of population subdivision upon individual pedigree inbreeding levels and total population levels of genetic variation can create difficult choices for managers. As we have seen, increasing gene flow between fragmented isolates has been stated as a priority for African rhinoceroses. Such gene flow has many beneficial effects from a population genetics perspective: it increases local population effective size (both N_{ef} and N_{ev}), it increases local levels of genetic diversity and hence the local adaptive flexibility, and it reduces the overall level of pedigree inbreeding, thereby minimizing the dangers of inbreeding depression. However, we must also recognize the conservation goal of maintaining high levels of genetic diversity in the total population for long periods of time. This goal may be achieved by allowing fragmentation of the population into isolates and avoiding translocations between existing fragments (Chesser, Smith & Brisbin, 1980). Thus there is a trade-off and genetic management decisions for the African rhinoceros species require a careful assessment of what the priorities are for each species.

Invoking franklin's 50/500 rule

Franklin's 50/500 rule was based on sound understanding of the different meanings of effective population size. Franklin's 50 referred to the inbreeding effective size, N_{ef}. This was meant to insure that there was sufficient variation in the founding population and that inbreeding depression could be avoided. The idea was to then breed the population up as fast as possible to reach a variance effective size, N_{ev}, of 500. This would insure that genetic loss because of the drift would be minimized. Both depend on the history of the population in question, but are often interpreted as referring to current census size or an inappropriate effective size (Walter, 1990). A tragic example may have been the use of census population size to suggest that, according to Franklin's rule, the northern white rhinoceros population was unlikely to survive (Walpole *et al.*, 2001). If their conclusion factored into the political and nongovernmental delays in taking action to protect that population, it would represent the most dramatic consequence of misunderstanding the terms discussed in this article.

Franklin's 50/500 rule also deals with loss of genetic variation in small populations because of the drift. Managers of captive populations can reduce drift by careful breeding, as Templeton & Read (1998) demonstrated in the Speke's Gazelle. In addition, wild populations with high fecundity and type I survivorship curves are likely to be less influenced by drift and more by selection. Lesica & Allendorf (1992) showed this by modelling the loss of heterozygosity in eight different species of plants with high reproductive outputs. They showed that as strong selection can weed out homozygotes with reduced viability, heterozygosity can be maintained even in small populations over many generations.

Finally, while the 50/500 rule only refers to the loss of genetic diversity, most population viability analysis models attempt to include loss of numbers resulting from demographic stochasticity as well as environmental stochasticity. When considering these factors, a population of 50 Baobab on Zanzibar will have a very different likelihood of surviving 100 years than a population of 50 chameleons on Lamu. Not only do the two populations have strikingly different demography, the impact of environmental stochasticity will differ significantly, as well. We also recognize that human politics and environmental policy can represent a significant component of environmental stochasticity for wildlife. The 1986 African rhinoceros conservation Conference in Cincinnati set the goal of conserving 2000 of each of the four black rhinoceros sub species. This was a census goal and not a goal for an effective population size. While that number may be related to insurance against demographic and ecological stochasticity, it is incomplete for understanding protection of genetic biodiversity in these taxa.

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