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**"Conservation Biology: The Ecology and Genetics  
of Endangered Species"**

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**These are preliminary lecture notes, intended only for distribution to participants.**

# Genes in Ecology

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## 17. CONSERVATION BIOLOGY: THE ECOLOGY AND GENETICS OF ENDANGERED SPECIES

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### INTRODUCTION

Population genetics and population dynamics are both crucial in the conservation and management of endangered species of animals and plants. However, a considerable change in emphasis occurs as we move from captive populations in zoos, through managed populations in nature reserves to whole communities of free-living organisms. Genetic considerations tend to guide the management of captive populations, while demographic, and often purely taxonomic, considerations tend to dominate studies of free-living populations and communities. To a large extent this continuum reflects the different types of information collected in studies designed to address different types of question.

This chapter attempts to partly redress the balance. First we review captive breeding in zoos where genetic conservation tactics are mainly concerned with maintaining a maximum level of genetic diversity. We then move on to discuss problems in free-living populations where both genetic and ecological considerations have been shown to be important. We conclude by discussing the relative time scales at which genetic, ecological and economic events affect endangered species, and the efficiency with which they can be managed. Throughout the chapter we emphasize areas where interactions between ecologists and geneticists will be important in improving the effectiveness of attempts to conserve endangered species. We centre our discussion around populations of large mammals but many of our conclusions will be relevant to other kinds of organisms.

## CAPTIVE POPULATIONS

In captive populations the primary management and research objectives are education and propagation, possibly for eventual reintroduction. Close genetic management is possible because individuals are usually both identifiable and under close management. Moreover, in many cases family relationships or sometimes extended pedigrees are available, and the capture site of wild caught individuals that founded the captive populations may be known. Increasingly, this kind of information is being recorded in zoo record systems, and for many endangered species stud-books and other databases that facilitate population management are maintained with detailed pedigree and other life history information on individuals (Olney 1980, Flesness & Mace 1988). Perhaps because of the availability of this kind of information, and the close control over the formation of breeding pairs that the captive environment presents, zoo breeding plans have tended to concentrate heavily on genetic management, especially based upon detailed pedigree analysis.

*Captive populations: detailed records available*

A variety of pedigree analysis methods have been applied but all involve tracing living individuals back to wild caught founders and calculating inbreeding coefficients. Generally the overall aims of genetic management are to maximize founder number, to equalize founder representation and to minimize inbreeding levels (Foose & Ballou 1988).

Founder animals are the source of all genetic variability in the population and the preservation of variation is generally the aim of captive management programmes. However, often little is known about the origins or relationships of founder animals and actual genetic information (e.g. from molecular studies) is rarely available. Genetic management, therefore, tends to be based around a simple though unrealistic assumption that all founders are genetically unique. Maximizing founder number and equalizing founder representation should maximize the probability of preserving genetic variation. Since inbreeding depression has now been demonstrated in a variety of both captive and wild populations (Ralls *et al.* 1979, Ballou & Ralls 1982, Ralls *et al.* 1988) minimizing inbreeding levels is another common aim. In a population with a completely known pedigree it should therefore be possible to design an ideal breeding plan. However, in reality there are a number of serious complications:

1 *Data are rarely complete.* Frequently there are unknown parents,

was recorded. When missing data are a relatively small fraction of the total it may be reasonable to fill in gaps with assumed events according to some 'worst case scenario' (Carroll & Mace 1988, Ballou in press). This is frequently done in captive management plans but it may influence the results of analyses quite markedly, especially where a significant portion of the pedigree is unknown. Under these circumstances it may be preferable to base management decisions on population-level analyses (see later). In the future we hope that molecular genetic data will contribute this kind of historical information, though there are methodological as well as technical difficulties (Lynch 1990).

2 *Pedigrees are bottlenecked and complex.* Often the pedigrees of captive populations are extended over many generations with cross-generation mating, periodic bottlenecks and extensive inbreeding. Under these circumstances, analytical methods for calculating relationship coefficients are inaccurate. For example, in the pedigrees in Fig. 17.1, all the living individuals have the same level of relationship to founder animals, and all founders have four living descendants. However, the probability that founder genes are preserved will vary. With inbreeding and family size variation, equalizing founder representation will tend to lead to multiple copies of the same founder genes, rather than maximizing genetic variation in the living population. To take this into account, pedigree simulation methods, known as 'gene dropping' are used to establish target representation levels for each founder based upon the probability that a founder allele is expected to be preserved in the living population (see MacLuer *et al.* 1986, Lacy 1989).

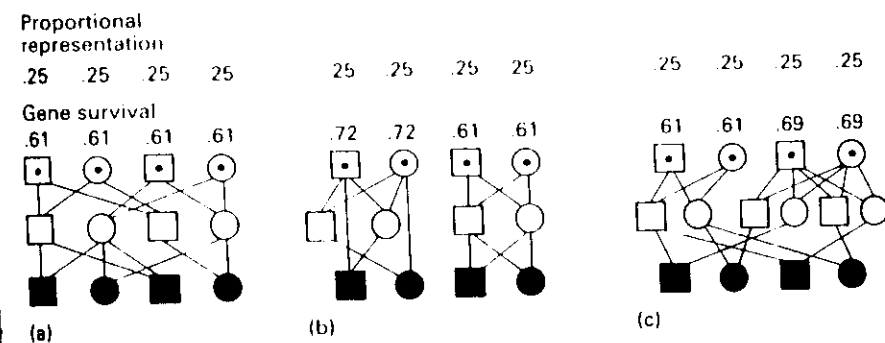


FIG. 17.1. Three simple pedigrees (a, b, c) in which two founder males (□) and two founder females (○) leave two surviving male (■) and female (●) offspring. Although the proportional genetic representation in the surviving population is the same for each founder, the probability that any one founder gene survives (gene survival) varies with the amount and nature of inbreeding and backcrossing (pedigree b) and on family size (pedigree c). See MacLuer *et al.* (1986) for more information.

**3 Inbreeding depression versus optimal outbreeding.** Evidence for inbreeding depression is now widespread from studies of captive, laboratory and wild populations (Ralls *et al.* 1979, Ralls & Ballou 1983, Ralls *et al.* 1986). However, several authors have suggested that minimization of inbreeding may not necessarily be best. Most natural populations are subdivided and outcrosses could potentially lead to the loss of locally adapted genotypes or to reduced fertility due to the breakdown of intrinsic genetic coadaptation (see Templeton 1986). These processes are often called 'outcrossing depression', though actual examples are rare. The most commonly cited case of outbreeding depression through loss of a locally adapted genotype concerns the unsuccessful translocation of ibex subspecies from Austria and Sinai to the Tatra mountains in Czechoslovakia, where the native subspecies had gone extinct. The introduced population rutted early and young were born in the coldest part of the year and died, leading to the extinction of the population (Greig 1979, Templeton 1986).

Intrinsic coadaptation refers to the way in which genetic or karyotypic characters are expected to evolve in response to others in the population, so that outcrosses could lead to the breakdown of these coadapted complexes. This process has been extensively studied in *Drosophila* (Templeton 1986) and plants (Ledig 1986) but is rarely documented in vertebrates. One clear-cut case is seen in captive populations of the douroucouli (*Aoniscus trivirgatus*) where chromosome studies have revealed polymorphisms in chromosome number both within and between different wild populations (de Boer 1982). Fertility is likely to be reduced from crossing some chromosome races because of difficulties at meiosis.

The degree of inbreeding depression or 'outcrossing depression' that a population will suffer will partly be a function of its recent history. Templeton *et al.* (1986) suggest a method to determine the impact of each in a captive pedigree as a prelude to devising a detailed management plan. In a recent study that adopted this method on 40 pedigrees of captive mammals, nine showed statistically significant inbreeding depression, but none showed significant outbreeding depression (Ralls *et al.* 1988). Inbreeding depression is probably a more significant factor in genetic management than outcrossing depression.

**4 Dealing with real animals.** Genetic management plans have to consider practical limitations imposed by economics, legislation, the logistics of zoo management, and most significantly by the behaviour of the species and individual animals involved in the programme. Behavioural considerations are extremely important, not only because failure to recognize them can lead to reduced viability and fertility, but also because inappro-

priate genetic management can have negative consequences. For example, polygynous species are subject to both natural and sexual selection but genetic management schemes based around the preservation of heterozygosity *per se* may tend to select against sexually selected characters perhaps to the detriment of population survival (Arnold in press). Polygynous species generally present more difficulties, especially in restricted populations where single males have dominated breeding over many breeding seasons.

Table 17.1 shows estimates of variance in life-time reproductive success for a selection of species maintained in captivity for which long-term data are available. The standardized variance ( $\sigma^2/\bar{x}^2$ ), denoted by  $I$ , is used to reflect the potential for selection among individuals (Arnold & Wade 1984a, b). The estimates were based on individuals whose whole life-time was recorded, except for the Asian lion (*Panthera leo persica*) where all individuals that had a breeding lifespan over at least 5 years were included. Compared with similar data on wild African lions (*Panthera leo*) (Packer *et al.* 1988) variances for both males and females are significantly higher in captive than in wild animals (males: wild  $I = 1.18$ , captive  $I = 4.27$ ,  $F_{36,90} = 3.82$ ,  $p < 0.001$ ; females: wild  $I = 0.41$ , captive  $I = 4.40$ ,  $F_{30,51} =$

TABLE 17.1. Estimated life-time reproductive success for seven captive species. For each sex the sample size ( $N$ ), mean ( $\bar{x}$ ), variance ( $\sigma^2$ ) and standardized variance ( $I = \sigma^2/\bar{x}^2$ ) are shown. Data analysed are from published data in international studbooks (see Olney & Ellis 1990 for details)

Species	Sex	$N$	$\bar{x}$	$\sigma^2$	$I$	$I_m/I_f$
Red-crowned crane	m	30	3.10	9.10	0.95	1.41
	f	42	2.70	4.80	0.66	
Pink pigeon	m	72	2.38	11.21	8.50	1.18
	f	91	1.11	5.71	4.66	
Asian lion	m	37	2.70	31.10	4.27	0.97
	f	60	2.78	31.00	4.40	
Grevy's zebra	m	75	3.60	34.00	2.63	3.70
	f	209	1.30	1.20	0.71	
Przewalski horse	m	108	1.40	23.44	11.96	3.16
	f	182	1.62	9.92	3.78	
Scimitar-horned oryx	m	103	2.18	127.90	26.90	6.18
	f	65	1.55	10.44	4.35	
Golden-headed lion tamarin	m	94	1.15	7.27	5.49	1.18
	f	91	1.11	5.74	4.66	

10.86,  $p < 0.001$ ). Comparable species were not otherwise available for direct comparison, but Fig. 17.2 shows standardized variances for a range of wild species compiled by Clutton-Brock (1988a) compared with the captive species in Table 17.1. For both sexes, higher variances are common in captive species. The reasons for this probably lie in low adult mortality in captive species and the tendency for some individuals to continue to dominate breeding over long time periods. High juvenile mortality may be a confounding factor in the estimation of  $I$  in both captive and wild species (Clutton-Brock 1988b) but would not be sufficient to explain the differences in Fig. 17.2. Whereas the variation observed in the free-living populations reflects differences in the breeding systems of the species, the

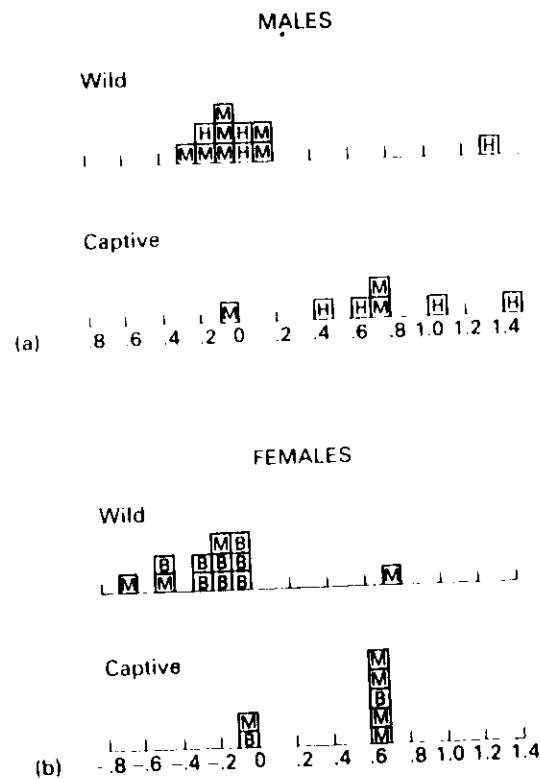


FIG. 17.2. Frequency distributions of log (standardized variance in reproductive success) for free-living species (wild) and seven captive species. The wild data are those compiled by Clutton-Brock (1988a). (a) Males: M, monogamous; H, harem. (b) Females: M, mammal; B, bird.

data from captive populations are due to differences in management practice that do not necessarily reflect the natural breeding system, and will result in strong selection pressures for certain traits that may well not be adaptive in more natural circumstances.

**5 Planning for the future.** Pedigree analyses are by definition retrospective but for conservation-sensitive species the analyses should be able to provide statistics useful for future planning. Although gene drop methods can provide some of this kind of information (MacLuer *et al.* 1986) and new methods are now being developed to identify genetically important individuals in a population (Ballou *in press*), many genetic plans are still based around quite general models predicting loss of genetic variability (heterozygosity) over specified time periods with given effective population sizes (Soulé *et al.* 1986). These methods are dominated by the effects of genetic drift and do not incorporate the effects of selection or population subdivision, both of which are likely to be significant.

#### *Captive populations: individuals and breeding not completely known*

In the case of many group-living species in captivity, and many wild populations, detailed studies can only provide a limited amount of information and this is never likely to be as complete as the full pedigrees discussed earlier (p. 406). Although genetic management will have similar aims in these populations, it has to be based upon population rather than individual data. The key statistic used in the genetic management of this type of population is effective population size,  $N_e$ , an estimate of the number of unique genetic individuals in the population contributing to subsequent generations. This can be estimated from breeding data on the mean and variance in family size for males and females (Lande & Barrowclough 1987, Harris & Allendorf 1989).

In theory,  $N_e$  may be greater than  $N$  (the census size) in a closely managed population but this is only achieved in very closely controlled circumstances, e.g. with laboratory animals (Falconer 1981). Estimates of  $N_e/N$  in natural and captive populations, based on demographic data are generally in the range 0.2–0.6 (Mace 1986, Carroll & Mace 1988). Nunney (1991) has shown that a good approximation of  $N_e$  is found simply from  $0.5 N_b$ , where  $N_b$  is the number of breeding individuals. However, some recent studies based on genetic data suggest that these are overestimates (e.g. Tomlinson *et al.* 1991) and in a recent study of large *Drosophila* populations  $N_e/N$  ratios were rarely more than 0.2 and usually less than 0.1 (Briscoe *et al.* *in press*). These differences are important because species conservation plans are usually based on assumptions about  $N_e/N$

ratios (Soulé *et al.* 1986, Lande & Barrowclough 1987, Mace & Lande 1991).

## THE POPULATION BIOLOGY OF INTENSIVELY MANAGED SPECIES

Genetic management has tended to dominate techniques for population management in captivity. However, this bias may not be appropriate in more natural environments (or in captivity). Demographic extinction factors are more difficult to quantify but simulation studies suggest their impact may be more significant in the short term. Here we present an example that uses data from some small populations of rhinos in Kenyan game sanctuaries.

### *Black rhino populations in Kenya*

Black rhinos (*Diceros bicornis*) are now threatened across their entire range (IUCN 1990); in East Africa no single population numbers more than 60 animals (Brett 1990). Some of these populations are in closely protected sanctuaries or reserves where detailed population monitoring is now under way. Their continued survival is critical for the species and population simulation studies are being undertaken to aid effective population management. Preliminary analyses presented here allow an insight into the significance of demographic and genetic factors in extinction rates, and the ecological and behavioural factors that will need to be taken into consideration in management strategies.

We have used the GAPPS animal population modelling software which is a discrete time, stochastic computer program that follows the history of each individual from birth to death (Harris *et al.* 1986). Input is in the form of a series of data files containing identities and parentage of each individual, age and sex-specific rates of survival and reproduction as well as rates of immigration of different age and sex classes. Data from rhino sanctuaries were used as input, and the populations were modelled for 200 years with no immigration or with one immigrant every 10 years up to year 50. The immigrant was set to be aged between 8 and 14 years, and to have an equal probability of being male or female. GAPPS also allows inbreeding depression to be modelled by adjusting the age-specific probability of survival or reproduction ( $P$ ) to be reduced according to the function:

$$P \times e^{-(bF)}$$

where  $F$  is the animal's inbreeding coefficient, and  $e$  is the base of natural logarithms.  $b$  is the slope of the line relating some fitness character to the level of inbreeding. In a set of 40 populations studied by Ralls *et al.* (1988),  $b$  was found to vary between  $-0.68$  and  $15.16$  with a mean of  $2.33$  and a median of  $1.57$  with juvenile survival as the dependent variable. In this study, female breeding rates were set as a function of  $b$ , and  $b$  was set to  $2.0$ , close to the median value for large mammals found by Ralls *et al.* (1988). The populations were modelled with and without inbreeding depression. Rates of breeding and survival were also adjusted by a function to incorporate density dependence. The carrying capacity of each reserve was estimated independently (Brett 1990) and at each breeding and survival event probabilities were adjusted by a modified Michaelis-Menton equation to:

$$\text{Min} + (\text{Max} - \text{Min}) \times (1 - [V^x / (0.05P_{95}^x + V^x)])$$

where Min and Max are the minimum and maximum probabilities allowed,  $V$  is an independent variable set to  $N$  (population size)/ $K$  (carrying capacity),  $P$  is the value of  $V$  at which the function takes a value 95% of the distance between Min and Max, and  $x$  is an exponent controlling the shape of the function (see Harris *et al.* 1986).

The results from two populations are presented here. The sanctuary population at Lewa Downs consists of 3 males and 10 females, 1 and 5 of which are adults respectively. The sanctuary is estimated to have a carrying capacity of 20. Nakuru National Park contains 11 males and 7 females, 8 and 5 of which are adults respectively, and has a carrying capacity of 71. Each population was modelled under three management options:

- 1 With no inbreeding depression and no immigration.
- 2 With inbreeding depression affecting female fertility and no immigration.
- 3 With inbreeding depression and immigration.

Population survival, population size and structure, average neonatal inbreeding coefficients and heterozygosity were recorded over 200 years; each simulation was repeated 200 times. The results are summarized in Figs 17.3 and 17.4.

Population survival for both populations was lowest in option 2, with 26% survival at Lewa Downs and 78% at Nakuru. The comparison between options 1 and 2 give insight into the relative significance of demographic and genetic extinction factors over the 200-year period. The extinction rates for the two options are initially similar when demographic extinction factors dominate. After about 100 years at Lewa Downs and 60 years at Nakuru the extinction curves diverge and inbreeding depression

starts to have a significant impact (Fig. 17.3). Two general conclusions may be drawn. In the short term, i.e. the next few decades, demographic extinction factors are more significant and it is only after this time that genetic considerations become important. Secondly, demographic extinction is considerably more of a threat to the smaller population at Lewa Downs than at Nakuru.

Even low levels of immigration by unrelated individuals have quite a major effect on population size and persistence. Once immigration was

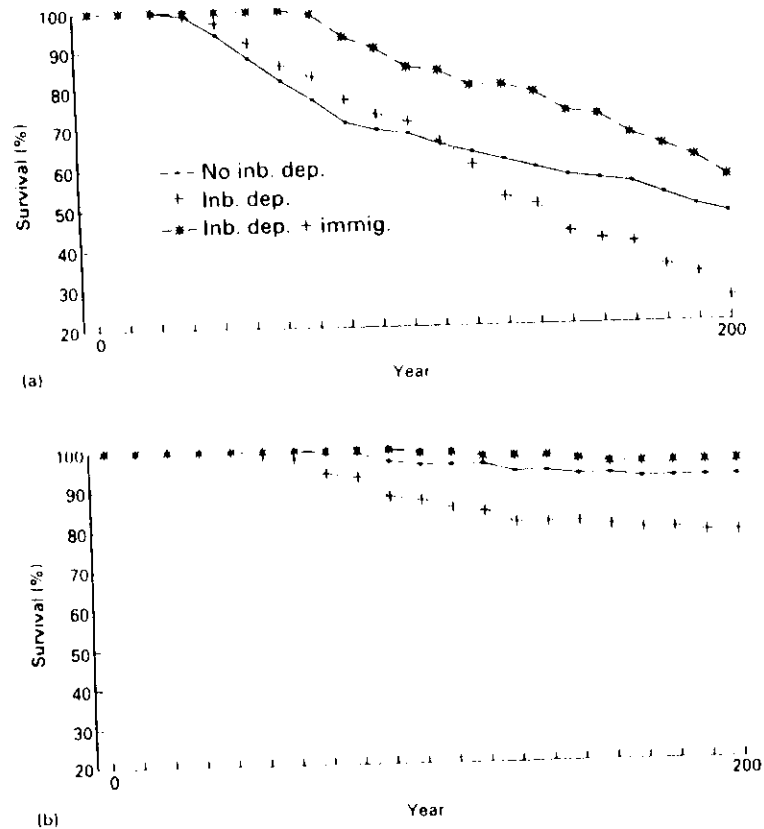


FIG. 17.3. The effect of inbreeding depression (Inb. dep.) and immigration (immig.) on the survival of populations of rhinoceros at Lewa Downs (a) and Nakuru National Parks (b). In both cases the probabilities of the present population surviving over the next 200 years are considered assuming no inbreeding depression, when extinction would be due entirely to stochastic events; inbreeding depression which lowers the survival of offspring as heterozygosity decreases; and immigration of new individuals into the population for the first 50 years of the project.

stopped, these benefits deteriorated quite rapidly due to inbreeding depression. At both Lewa Downs and Nakuru this option led to the highest persistence rate at 200 years (Fig. 17.3). However, 100 years after immigration has ceased the population sizes were again low and similar to those achieved with no immigration (Fig. 17.4). It was only under option 1, with no inbreeding depression, that population size was maintained close to carrying capacity after about 150 years. Two general conclusions can be drawn from this analysis. In small populations demographic forces are likely to dominate rates of extinction but even low levels of immigration can have a significant beneficial influence, especially by reducing the demographic extinction factors and delaying the effects of inbreeding depression. These benefits deteriorate rapidly once immigration is halted.

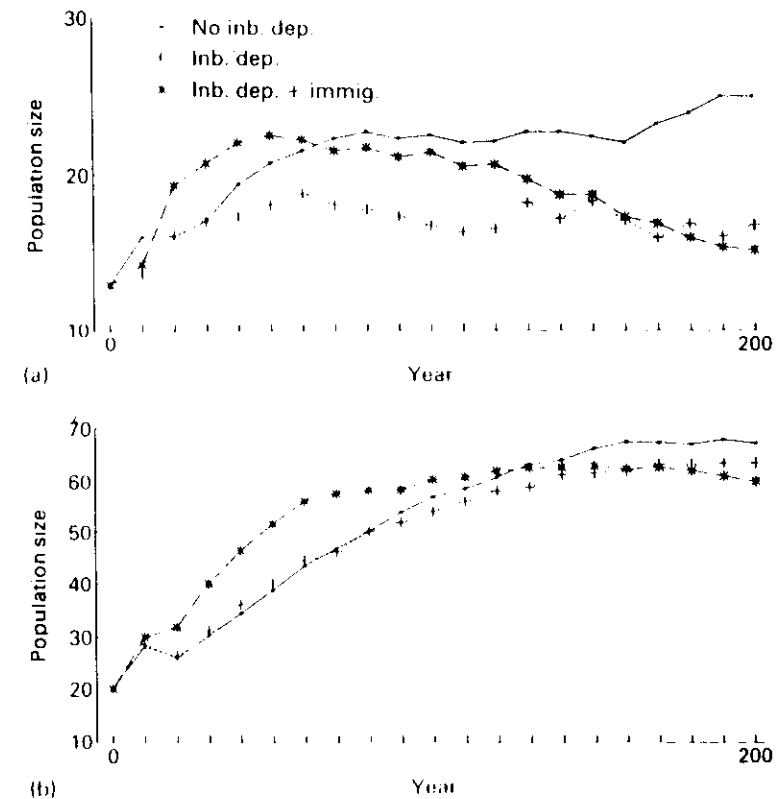


FIG. 17.4. The effect of inbreeding depression (Inb. dep.) and immigration (immig.) on the size of populations of rhinoceros at Lewa Downs (a) and Nakuru National Parks (b). In both cases the average size of the population over the next 200 years is illustrated under the same set of assumptions as were used in the simulations of Fig. 17.3.



In very small populations, such as that at Lewa Downs, the effect is particularly marked. However, in all small populations genetic factors will eventually become significant.

These models are relatively simple and the results should not be taken too literally. In several ways the population survival rates are likely to be overestimates. The model does not incorporate the effects of extrinsic extinction factors such as disease, food supply failure or loss of more habitat, all of which are likely to influence all populations throughout time. Secondly, the simulation assumes that mating pairs are selected at random, thus ignoring the influence of male dominance and territoriality characteristic of the species; in natural populations this will generally lead to higher levels of relatedness and hence more pronounced inbreeding depression. The model does not allow any adaptation to inbreeding depression in the population; this might be expected over the course of several generations of inbreeding (Templeton & Read 1983), and would tend to slow down the deleterious genetic effects that dominate the dynamics towards the end of the 200-year period.

A general conclusion is that most of these small populations in Kenya are non-viable without intensive management, involving continuous monitoring of population size and structure and periodic introduction of unrelated individuals. Applying these recommendations presents a series of practical difficulties resulting from the ecology and behaviour of the species (Brett 1990). In many areas the vegetation is extremely dense and monitoring individuals is difficult and dangerous. Immobilization of individuals for monitoring or transfer is difficult and costly with high risks to both rhinos and biologists. Considerable aggression from resident animals may pose problems for immigrants, especially for older animals. Finally, habitat differences in browse, disease, temperature, disturbance, etc., may pose adaptational problems for new immigrants. All these factors will have to be quantified and costed in the future as the biological factors clearly indicate that unless some kind of intensive management is undertaken these small populations are not viable.

#### THE DEMOGRAPHY OF FREE-LIVING ENDANGERED SPECIES

The diversity of problems facing population biologists interested in conserving endangered species is nowhere more acutely apparent than when we consider the primates. Current estimates suggest that more than 50% of the 230 extant primate species may become extinct sometime in the next 20–50 years (Mittermeier *et al.* 1986). The world population size of

many primate species is smaller than that of most towns or villages (Jolly 1985). Although nearly all species have now been studied in the wild, the average duration of a primate field study is less than 3 years; this is considerably less than the life expectancy of most primate species and close to the average interbirth interval of most (Dobson & Lyles 1989). The demographic data available for most primate populations is scant at best and there are almost no studies of the genetics of wild primate populations. Nevertheless, the recent rapid developments in DNA fingerprinting technology should allow the reconstruction of pedigrees from long-term studies of primates and other species in the wild.

Merenlender and Dobson have begun such a study at Ranomafana National Park in Madagascar, and we hope to compare the demography *and* genetics of two closely related lemur species with different social systems. One particular irony of the study is that the techniques for genetic analysis develop at a much faster rate than the data accumulates. When the study was initiated we concentrated on determining if Jeffrey's probe could be used to construct pedigrees for captive populations of lemurs (Jeffreys *et al.* 1985). As the field study developed we realized that serious ambiguities could result in our assessment of paternity if we relied on these techniques (Lynch 1990), and we have subsequently developed single-locus probes with which to undertake these studies. The advent of the polymerase chain reaction (PCR) means that we could do many more things with the limited amount of tissue collected in the field. It is a full-time job keeping up with the genetic techniques and there is a constant temptation to adopt new techniques before we have used those available to address our initial questions.

The extensive marking and monitoring of animals required by the study has already revealed something that would have taken considerably longer in a more conventional primate field study: *Lemur rubriventer*, previously supposed to be monogamous, frequently change mates between breeding seasons; in contrast, *L. fulvus rufus* have very stable group structure. The full implications of these differences between social systems for the genetic structure of the population will become apparent as the study progresses.

#### SELECTION IN EXPLOITED POPULATIONS OF ENDANGERED SPECIES

Many endangered populations have become reduced in numbers through human exploitation. Economic analyses indicate that it is often in the interest of those exploiting a population to use it to the brink of extinction

(Clark 1976, Walters 1986). Intense selection may ultimately lead to genetic changes in the population that allow it to better withstand the impact of humans. However, the time scale at which the population responds to selection may be considerably longer than either the time scale determining changes in numbers or the time scale at which economic markets create opportunities for exploitation. An analysis of a hypothetical gene for tusklessness in elephant populations can illustrate these problems.

#### *Elephants, ivory and poaching*

The African elephant, *Loxodonta edentata*, was recently declared endangered on a global scale and placed on Appendix 1 of Convention on Trade in Endangered Species (CITES), resulting in a complete ban on trade in elephant products by all the countries that are signatories to CITES. The ban was initiated following a series of analyses which suggested that elephants would be driven to extinction in many parts of Africa if poaching continued at the rates prevalent in the early 1980s. Levels of trade in ivory had been increasing rapidly following increases in the price of ivory over the last 30 years (Fig. 17.5). The huge volume of ivory moved through the markets was observed to consist of tusks from increasing numbers of smaller individuals, suggesting that the demand for ivory had led to a switch from the older males to immature males and females (Poole & Thomsen 1989). By the mid-1980s the volume of ivory entering the trade was diminishing rapidly suggesting that stocks were rapidly being overexploited. Field surveys recorded widespread decreases in the size of Africa's elephant populations (Douglas-Hamilton 1987).

The demography of African elephants has been examined using a number of mathematical models (Caughley *et al.* 1990, Basson *et al.* 1991, Milner-Guillard & Mace 1991, Dobson & Poole in preparation). A variety of sources suggest that both age at first reproduction and interbirth interval are dependent upon available resources (Fig. 17.6; Laws 1969, Eltringham 1982). These density dependent relationships can be readily included into age-structured (Leslie matrix) models and stock recruitment relationships derived for elephant populations under different exploitation assumptions. The simplest (and least accurate) way to do this is to assume random harvesting (Fig. 17.7). Such models suggest that elephant populations may be driven to extinction by harvest levels in excess of 6% per annum. Furthermore, the time taken to drive populations to extinction decreases rapidly as annual exploitation rates exceed 10% per annum. Estimates of average exploitation rates for the late 1970s and early 1980s suggest that poaching levels may have been as high as 15–20% per

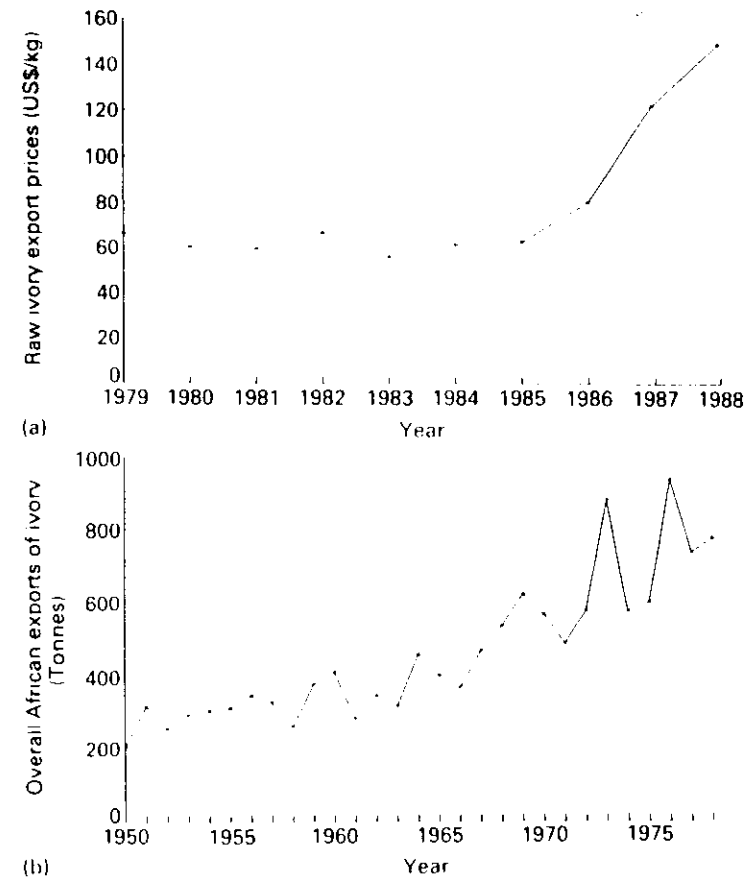


FIG. 17.5. (a) The raw ivory export prices for the years 1979–1988. (b) The amount of ivory exported from Africa in the years 1950–1978. (After Barber *et al.* 1990.)

annum (Milner-Guillard & Mace 1991); had this continued it would have driven elephants to extinction by the beginning of the next century.

The models of elephant demography can be modified to consider rates of gene frequency change under exploitation. There is empirical evidence to suggest that tusklessness has increased in frequency in heavily poached populations (Fig. 17.8; Douglas-Hamilton personal communication, Hall-Martin 1980). Tusks have also completely disappeared in female Indian elephants (Sukumar 1990). In this example we consider a simple one locus, two allele model for tusklessness. We assume that tusked is the dominant trait and that tusklessness is only expressed in homozygous

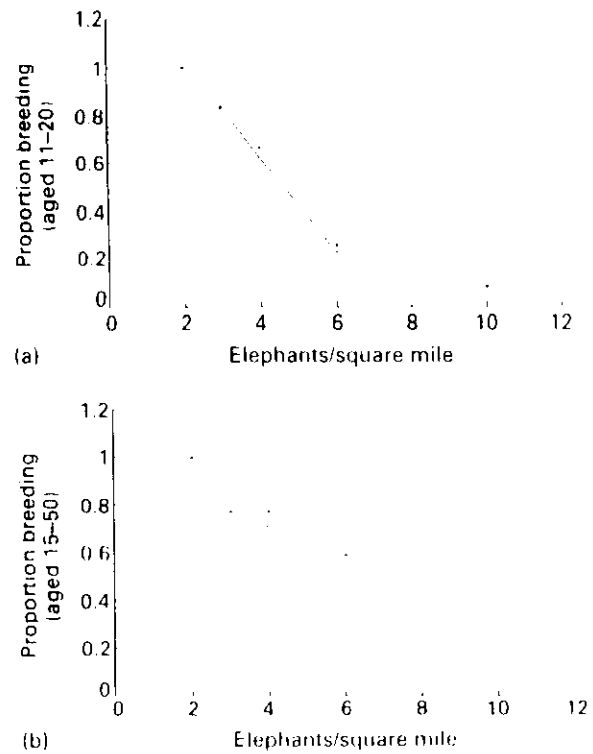


FIG. 17.6. The observed relationship between age at (a) first reproduction and (b) interbirth interval for African elephants (data from Laws 1969). Fecundity is expressed as the proportion of female elephants breeding in any time interval.

recessive individuals. Because male elephants use their tusks in fights to control access to females, we assume that the fitness of a tuskless individual is a function of their frequency in the population. When tusked individuals are common, tuskless individuals are unable to win fights and fail to obtain matings, as the frequency of tusked individuals is reduced by poaching, the relative ability of tuskless individuals to obtain matings increases (Fig. 17.9). In the absence of poaching, tuskless individuals only appear in the population when two heterozygous individuals mate and produce an offspring. The model is obviously a caricature of reality. However, in the absence of any real information on the genetic mechanisms determining these traits in elephants, it acts as a phenomenological example which serves to illustrate the rate at which gene frequencies respond to selection in populations with this type of age structure.

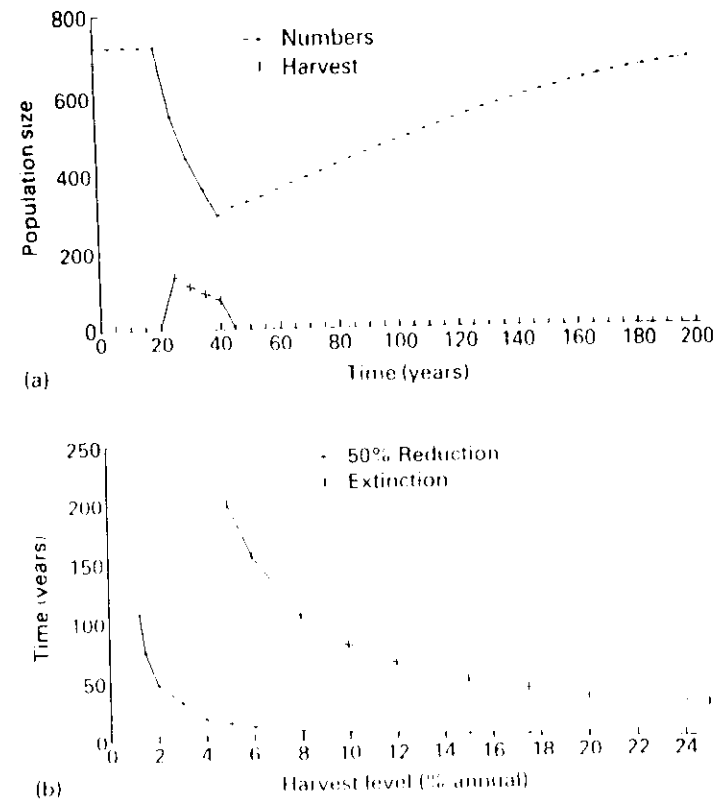


FIG. 17.7. (a) The effect of randomly harvesting 5% of the elephants in a population over a 20-year time interval. The upper line shows total population size, the lower shows resultant ivory yield. (b) The time taken to reduce an elephant population by 50% and to drive it to extinction at a range of different harvesting levels. (After Dobson & Poole in preparation.)

The initial conditions for the simulations were determined by running the model in the absence of poaching until all age classes and gene frequencies arrived at stable numbers and frequencies, these were then used as the initial conditions for the exploited population. In the absence of any selection for tusks, random harvesting of the population at an annual level of 5% is sufficient to drive the population almost to extinction (Fig. 17.7). In contrast, when only tusked individuals are removed from a population containing genes for tusklessness, the population initially declines to a low level where it remains stable for around 200 years (Fig. 17.10). During this time the relative frequencies of tusked and tuskless genes changes. Eventually, the mating success of the tuskless individuals

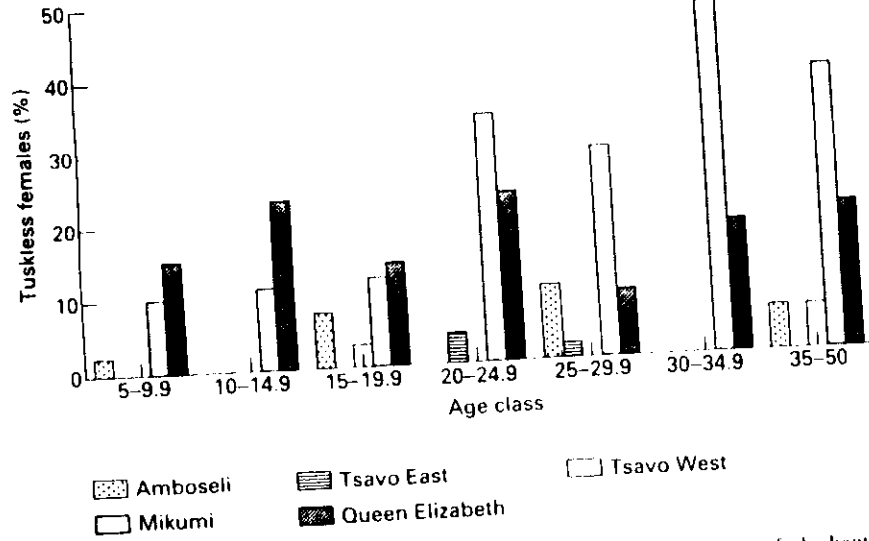


Fig. 17.8 The numbers of tuskless individuals observed in four populations of elephants surveyed by Poole (unpublished). The Amboseli population is relatively unpoached, the populations in Tsavo, Mikumi and Queen Elizabeth Parks have been subjected to increasing levels of poaching.

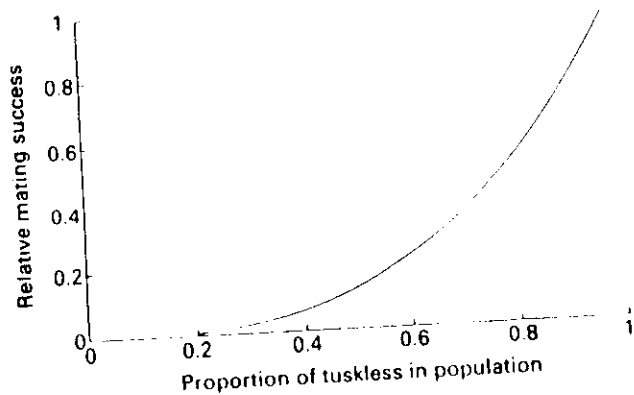


Fig. 17.9. Hypothetical relationship between the relative number of matings obtained by tuskless individuals as a function of their frequency in the population. The graph assumes that tusked males have an average relative mating success of unity.

approaches parity with the tusked individuals, and the tuskless population increases to the carrying capacity of the previously predominantly tusked population. The most important point to emerge is that even in the face of intense selection, rates of gene frequency change are slow when

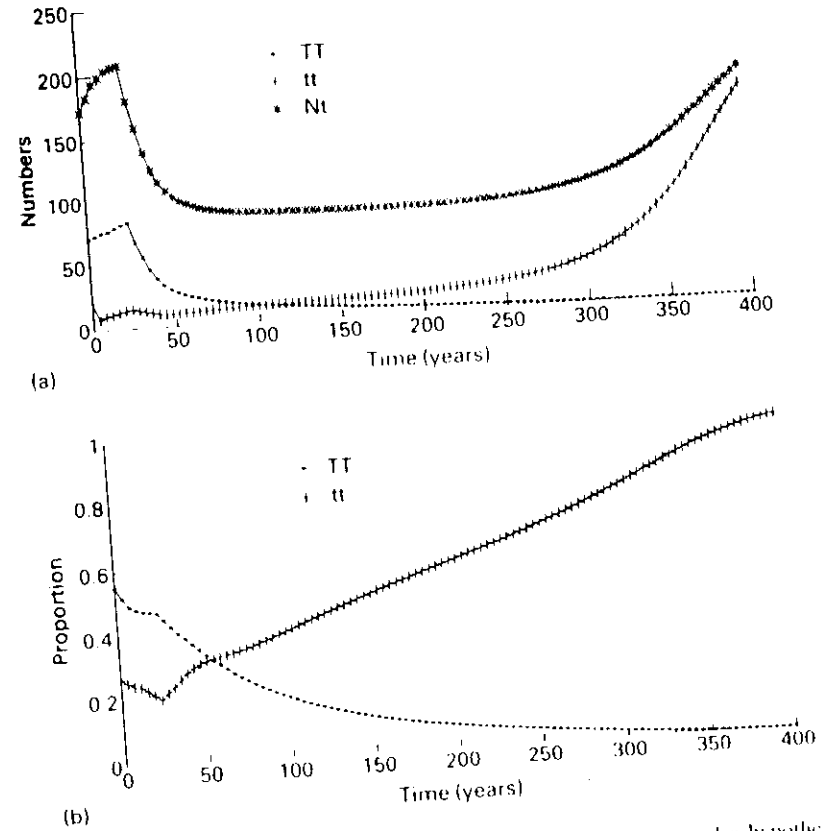


Fig. 17.10 The effect of a 5% harvest rate on the total population size of a hypothetical elephant population. (a) The total numbers of individuals ( $N_t$ ) and the numbers homozygous for tusked ( $TT$ ) or tuskless ( $tt$ ). (b) The frequency of the tusked and tuskless alleles.

compared with the changes in population density. The age structure of the elephant population gives the species considerable resilience to selection operating over quite long time intervals.

It is also possible to examine what happens if we stop harvesting the population once it has reached either a low density or after the tusked trait is almost completely removed from the population (Fig. 17.11). In both cases the frequency of tusked individuals increases and ultimately their frequency and numbers return to a stable polymorphic frequency. However, this adjustment takes over two to four centuries, a period of time considerably longer than the time scale at which the elephants respond to exploitation.

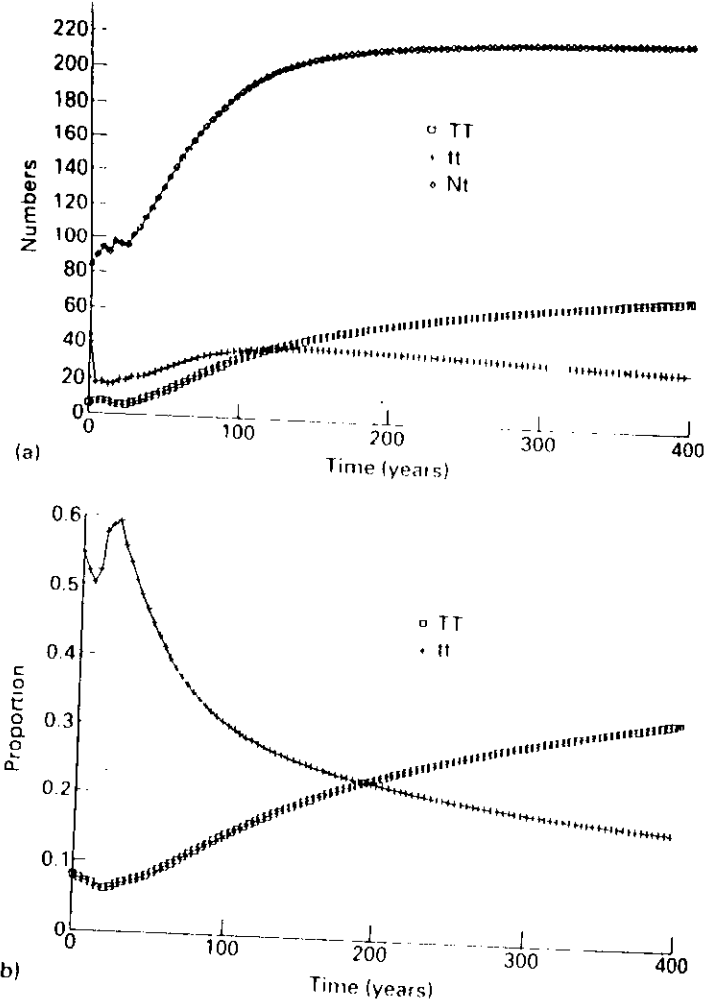


FIG. 17.11. Recovery of a previously harvested population from its minimum density. (a) The total numbers of individuals (Nt) and the numbers homozygous for tusked (TT) and tuskless (tt) conditions. (b) The frequency of the tusked and tuskless alleles.

*The effect of elephant social systems on demography*

The models can be further modified to examine the effect of elephant social systems on demography (Dobson & Poole in preparation). Inclusion of different features of elephant social systems (mate choice, allomothering) into population models always produce an Allee effect, a deterministic

threshold below which the populations collapse to extinction. These thresholds, or breakpoints, were originally postulated to occur for parasitic helminths (May 1977). They have also been examined in models for primates where the magnitude of the breakpoint is dependent on the social system of the species. In general, monogamous, more solitary species tend to have higher thresholds than group-living promiscuous species (Dobson & Lyles 1986). The magnitude of these thresholds will also be important in determining the size and composition of populations that are reintroduced to the wild. Furthermore, in declining populations, the social structure of the population may be such that the population may be in danger of deterministic collapse at population sizes higher than those where inbreeding has a significant effect on viability.

An important additional exercise is to examine the impact deterministic Allee effects have on rare alleles in more complex genetic models. Unpublished work by Gupta *et al.* (personal communication) on selection in parasite models suggest these 'Allee-type' effects lead to enhanced rates of loss of heterozygosity at densities where drift may not be leading to significant losses. Inclusion of these effects into estimates of  $N_e$  might perhaps explain some of the anomalies between observed and estimated values of  $N_e/N$  discussed earlier (Dobson in preparation).

ECONOMICS, GENES, ECOLOGY AND CONSERVATION

All of the analyses discussed in this chapter suggest that the conservation and management of endangered species present a number of problems that require further interactions between ecologists and geneticists. In each of the four areas described earlier, more basic scientific information is required about the interactions between changes in population size and changes in levels of genetic heterozygosity. In particular, we need to know more about how human modification and reduction of natural habitats is likely to affect the persistence of increasingly fragmented populations and rates of gene flow between these populations. Consideration of human activities is crucial as most of the economic processes that encroach on natural populations and communities operate on a much faster time scale than the demographic and genetic events that determine the ability of any individual population to respond and adapt to changes in its natural environment.

Although captive breeding programmes have been developed for many endangered species, it is essential that some vestige of a truly natural habitat be available for the reintroduction to the wild that is the ultimate

aim of these programmes. Although captive populations of some animals have been successfully reintroduced into the wild (Stanley-Price 1986), the costs of maintaining species in captivity are significant and there is a definite limit on space in zoos and conservation centres (Conway 1986). The costs of captive propagation are dependent upon the social system of the species; solitary, territorial species usually cost more than more gregarious species (Table 17.2). Plans for captive propagation and release will ultimately only be successful if they proceed in conjunction with projects that maintain the integrity of the species' natural habitat in the wild. Reintroduction will only be successful if the habitat is maintained so that the reintroduced individuals can use resources in a way that is

TABLE 17.2. Comparative annual upkeep of 11 species maintained at an effective population size ( $N_e$ ) sufficient to sustain 90% of founder heterozygosity over 200 years. (After Conway 1986.)

Species	Generation time (years)	$N_e$	Annual upkeep (US\$ $\times 10^3$ )
Siberian tiger <i>Panthera tigris altaica</i>	7	136	57.7
Indian rhinoceros <i>Rhinoceros unicornis</i>	18	53	44.4
Nyala <i>Tragelaphus angasi</i>	8	115	15.3
Striped grass mouse <i>Lemniscomys striatus</i>	0.75	1275	13.1
Brush-tailed betong <i>Bettongia penicillata</i>	6	159	9.0
Mauritius pink pigeon <i>Bosoenas mayeri</i>	10	95	8.7
Arabian oryx <i>Oryx leucoryx</i>	10	95	7.8
African black-necked cobra <i>Naja nigricollis pallida</i>	10	95	6.3
Bullfrog <i>Rana catesbeiana</i>	7	136	4.0
White-naped crane <i>Grus vipio</i>	26	37	3.1
Caribbean flamingo <i>Phoenicopterus r. ruber</i>	26	37	1.1

beneficial to themselves and not excessively detrimental to the structure of the community (Lyles & May 1988).

The importance of social systems in determining both demographic and genetic effects is still an area that requires intensive collaborative studies if realistic species survival plans are to be assembled for endangered species. A better understanding is required of the role of social systems in determining both the size of populations where inbreeding effects become important and the interaction of this with deterministic and stochastic mechanisms which may cause populations to collapse to extinction.

All of the work we have discussed here requires more interactions between ecologists and geneticists. It seems unlikely that these collaborations will come to fruition unless more imaginative funding is available for interdisciplinary projects from research foundations. The predetermined scepticism of geneticists towards ecology, and vice versa, will have to be discounted by 'research boards' reviewing grants for interdisciplinary projects. Most major breakthroughs in science have come from hybrid projects that seek to cross-fertilize ideas from different disciplines. The conservation of the world's natural plant and animal resources requires fertile interactions not only between ecologists and geneticists, but also with economists, and even sociologists and politicians. If the ecologists and geneticists continue to have difficulties in communicating, there is little hope for the discussions between all of these groups that are required to provide viable means of managing natural populations of endangered species.

#### ACKNOWLEDGEMENTS

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## 18. GENES IN THE REAL WORLD

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### INTRODUCTION

Ecology and genetics have always been uneasy bedfellows, despite their intrinsic complementarity; genetics is about what exists, ecology is about how it exists. Darwin was uncomfortably aware of the need for a physical basis to variation, and the discoveries of genetics in the years following 1900 provided this (Fisher 1954). But the biometrical–Mendelist disputes of the 1900s, the geneticist–palaeontological debates of the 1920s and 1930s, and the neutralist controversies of the 1970s and 1980s have repeatedly forced the disciplines apart (Provine 1971, Mayr & Provine 1980). The chapters in this volume have explored the current situation, in particular the contribution that genetics can (and should) make to ecology and vice versa. In this concluding chapter, we seek lessons from the past and pointers for the future. Our conviction is that any understanding of the 'real world' will be incomplete and potentially distorted unless it is based on all relevant factors, and not merely those tractable to particular viewpoints.

### LEARNING FROM MISTAKES

Ecology lacks an agreed theoretical core and is therefore easily destabilized and subject to intellectual fashion. At times its development has been driven by deterministic models, ecosystem studies, energetics, physiological understanding and others (Berry 1989a); ecologists tend to carry personal prejudices from their own experiences, with the additional complication that 'very general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases' (MacArthur 1968).

It would be presumptuous (and reminiscent of past mistakes) to claim we have identified *the* key to ecology but we are impressed by the number of times that deterministic models tested (or often not) under