Ballou '89

Conservation Biology and the Black-Footed Ferret

Edited by Ulysses S. Seal
E. TOM THORNE
MICHAEL A. BOGAN
STANLEY H. ANDERSON

Yale University Press
New Haven and London

1989

pulations. In *Conservation*
E. Soule and B. A. Wilcox,

n vulnerability. In *Viable*
. Cambridge: Cambridge

populations: Processes of
of scarcity and diversity, ed.
sociates.
ction. In *Viable populations*
: Cambridge Univ. Press.
ography in the design and
es Modeling 1:205–34.
imum population size for
. *Memoirs* 8:150–59.
and captive propagation.

iation in the black-footed
45–49.
y in a polygenic character

population size, genetic
t. In *Viable populations for*
Cambridge Univ. Press.
tion in a varying environ-

rk: Harper and Row.
ory of island biogeography.

osystems. Princeton, N.J.:

ion of colonizing species.

A question of risk. *Trans.*

ammals. II. The red fox,
Mustela nivalis, the beech
ereditas 96:299–305.
. Cambridge: Cambridge

5

JONATHAN D. BALLOU

Inbreeding and Outbreeding Depression in the Captive Propagation of Black-Footed Ferrets

Captive propagation is a powerful tool in aiding the survival of endangered and threatened species (Conway 1980; Martin 1975). In recent years, new techniques for long-term genetic and demographic management have been developed (Dresser 1984; Flesness 1977; Foose 1983; Ralls and Ballou 1983). It is clear that in the case of the black-footed ferrets the priorities are demographic rather than genetic. As the captive population grows, however, genetic considerations will become more important.

This chapter discusses two genetic considerations important to the survival of the captive ferret population: inbreeding and outbreeding depression. Because both could significantly affect survival and reproduction in other captive populations, they should be addressed in the development of a black-footed ferret captive-breeding plan.

Inbreeding Depression

The deleterious effects of inbreeding on both reproductive and survival characteristics have been well documented in a large variety of domestic, laboratory, and captive populations. Wright's (1922) analysis of the effects of inbreeding in guinea pigs probably remains the most extensive study of inbreeding effects to date. During 18 years of experimental inbreeding of guinea pig colonies for the Department of Agriculture, Wright (1977) documented reduction in size and frequency of litters, a decrease in the proportion of animals born alive and reared to 3 months of age, and a decrease in birth weight and weight at 3 months of age (Wright 1977). Similar results have been shown in cattle (Young et al. 1969), pigs (McPhee et al. 1931), rabbits (Chai 1969), dogs (Wildt et al. 1982), and many other domestic animals (Ralls and Ballou 1983).

Few data are available on the effects of inbreeding in mustelids. Although inbreeding in domestic ferrets is a concern (Marshall, pers. comm.), data on the effects are not available. Johansson (1961) conducted inbreeding experiments on ranch-bred Swedish mink (*Mustela vison*). Mink ranches in Sweden have traditionally developed their mink populations from small numbers of wild-caught animals. This approach, in addition to selective breeding for coat color, has resulted in high levels of inbreeding in the ranch mink populations. Crossings between different strains, however, may have restored levels of heterozygosity. Despite the previous inbreeding in the population, additional inbreeding of these ranch-bred mink still resulted in reduced survivorship, reproduction, and litter size and was severe enough to cause extinction by the fourth generation in the experimental inbred lines (Fig. 5.1).

Information on the effects of inbreeding in nondomestic species

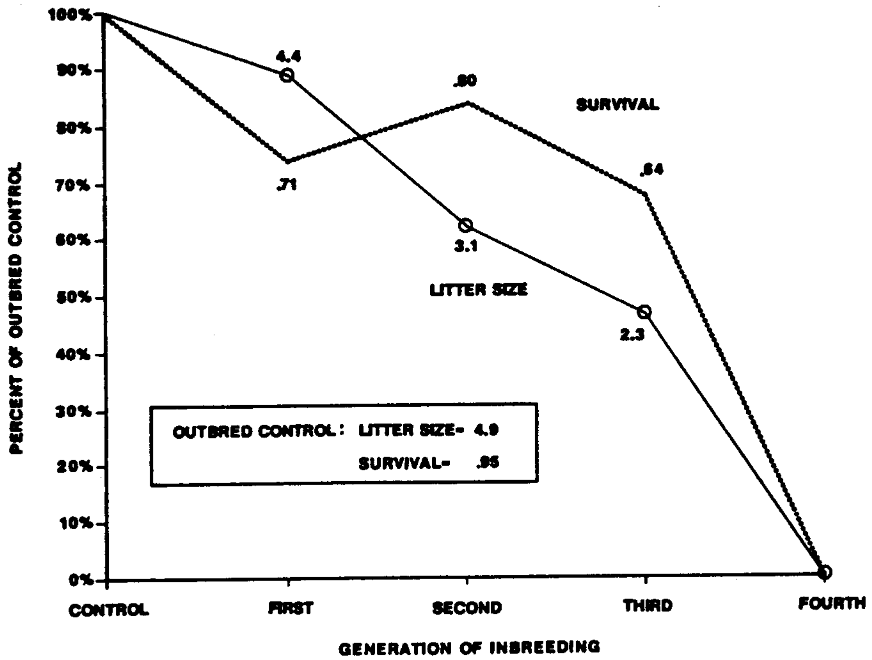


Figure 5.1. The decrease in survival and litter size in inbred mink. The mean effect of inbreeding in 8 lines of inbred mink at 4 mink ranches over 4 generations is shown as a percentage of the outbred control. Lines at 3 of the 4 ranches went extinct after the 2d generation, and the last lines survived only to the 3d. The number of offspring produced by the outbred controls and the 1st, 2d, and 3d inbred generations were 2,549, 157, 99, and 25, respectively (Johansson 1961).

---

comes primarily from b
tions. Ralls and her co
breeding on juvenile an
from 7 orders, 21 famil
tions had higher inbred
Fig. 5.2). Significant di
tality rates within popul
lations. Small sample si
the statistical power of a
clearly indicative of a ge
ing on captive mammal
port these conclusions (
Buisman and van Weer

Studies on the effects
Packer (1979) found re
parents; and evidence f
great tit (Bulmer 1973).

Data from studies co

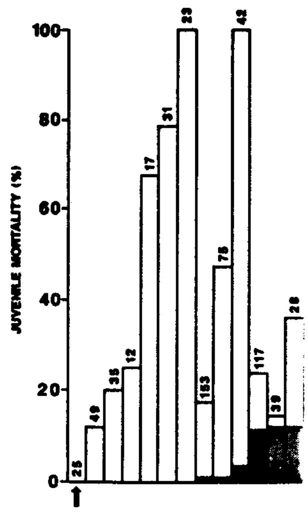
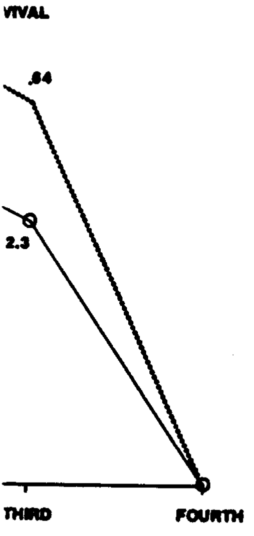


Figure 5.2. Inbred (shaded) a
populations (Ralls and Ballo
mortality rates. The numbers
represent the 3 populations t
(from left to right: four-stripe

ling in mustelids. Al-
cern (Marshall, pers.
hansson (1961) con-
vedish mink (*Mustela*
developed their mink
it animals. This ap-
color, has resulted in
lations. Crossings be-
red levels of hetero-
opulation, additional
ted in reduced sur-
vere enough to cause
imental inbred lines

nondomestic species



ink. The mean effect of
generations is shown as a
went extinct after the 2d
er of offspring produced
is were 2,549, 157, 99, and

comes primarily from breeding and pedigree records of captive populations. Ralls and her colleagues (1983) summarized the effects of inbreeding on juvenile and infant mortality in 44 mammalian populations from 7 orders, 21 families, and 36 genera. Forty-one of the 44 populations had higher inbred than noninbred juvenile mortality ($p = 0.001$; Fig. 5.2). Significant differences between inbred and noninbred mortality rates within populations were found in only 14 (31%) of the populations. Small sample sizes of most of the populations surveyed limited the statistical power of analyses (see below). Nevertheless, the results are clearly indicative of a general trend in the deleterious effects of inbreeding on captive mammalian populations. Numerous other studies support these conclusions (Templeton and Read 1983; Shoemaker 1982; Buisman and van Weeren 1982; Roberts 1982).

Studies on the effects of inbreeding in natural populations are scarce. Packer (1979) found reduced survival in baboon offspring from related parents; and evidence for inbreeding depression has been found in the great tit (Bulmer 1973).

Data from studies correlating the level of inbreeding on mortality and

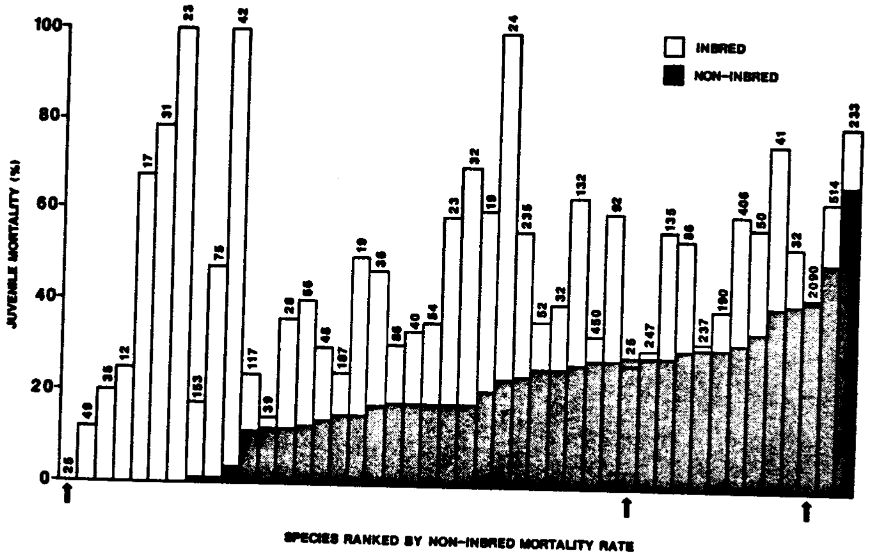


Figure 5.2. Inbred (shaded) and noninbred mortality rates in 44 different mammalian populations (Ralls and Ballou 1983). The populations are ranked by their noninbred mortality rates. The numbers represent total sample sizes in each population. The arrows represent the 3 populations that show higher (nonsignificant) noninbred mortality rates (from left to right: four-striped rat, kudu, and pig-tailed macaque).

reproductive characteristics in domestic species show an approximate 10 to 20% decrease in fitness with each 10% increase in inbreeding. Ralls et al. (1988) examined the correlation between inbreeding coefficients and mortality in 40 different captive populations. The mortality rates associated with different levels of inbreeding were calculated and regressed on the inbreeding coefficients within each of the populations. This method was analogous to that used by Templeton and Read (1984) in analyzing inbreeding effects in Speke's gazelle (*Gazella spekei*). The severity of the inbreeding effect (the number of lethal equivalents [Morton et al. 1956]) could then be estimated by the rate at which mortality increased with the increasing inbreeding coefficient (the slope of the regression). In addition, a predicted mortality rate for any specified level of inbreeding could be calculated using the estimated regression equation.

Figure 5.3 illustrates the distribution of the predicted increase in mortality associated with an inbreeding coefficient of 10% for the 40 populations surveyed (Ralls et al. 1988). Although the effect of inbreeding on early mortality was highly variable, a 10% increase in inbreeding caused an average 10% decrease in survival; 50% of the populations had predicted decreased levels of survival between 3% and 15%. Figure 5.4 shows the predicted relationship between inbreeding coefficients and survivorship for the median and the upper and lower quartiles of the distribution.

These figures probably underestimate the inbreeding effects that occur in wild populations. In captivity, weak inbred animals that benefit from veterinary care might be expected to have lower mortality rates than inbred animals in the wild. Nevertheless, these results illustrate the potential effect inbreeding can have on mortality rates in captive mammal populations, as well as the variation in responses to inbreeding within different populations.

The loss of heterozygosity due to inbreeding can be directly correlated with fitness components such as survival and reproduction in captive populations with known pedigrees. In populations without pedigrees, evaluating the potential effects of the loss of heterozygosity is much more difficult. Evidence of inbreeding depression in these populations is indirectly inferred from studies on the relationship between heterozygosity and fitness. If such a positive relationship does exist, the loss of heterozygosity due to inbreeding, genetic drift, or other factors will result in a population with lower fitness.

Several studies show that there is a general, though not universal, positive relationship between heterozygosity and various fitness components (survivorship, disease resistance, growth and developmental rate,

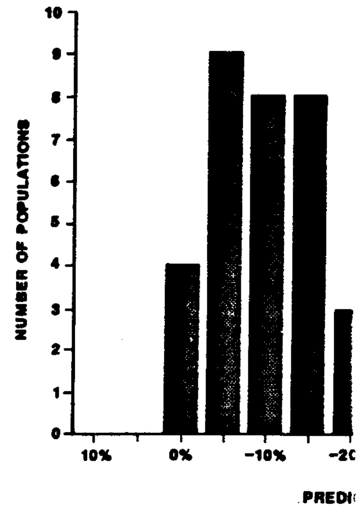


Figure 5.3. The predicted change in
40 mammalian populations (Ralls e

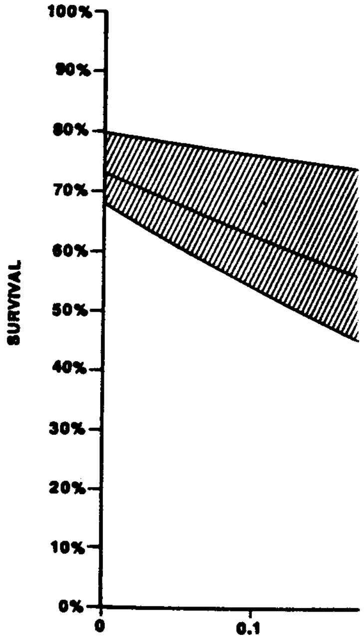


Figure 5.4. The predicted relations
malian populations (Ralls et al. 1988).
distribution of 40 populations are sh

ic species show an approximate
10% increase in inbreeding. Ralls
between inbreeding coefficients
opulations. The mortality rates
eeding were calculated and re-
within each of the populations.
l by Templeton and Read (1984)
ke's gazelle (*Gazella spekei*). The
number of lethal equivalents
mated by the rate at which mor-
reeding coefficient (the slope of
l mortality rate for any specified
using the estimated regression

n of the predicted increase in
g coefficient of 10% for the 40
Although the effect of inbreed-
le, a 10% increase in inbreeding
ival; 50% of the populations had
etween 3% and 15%. Figure 5.4
en inbreeding coefficients and
pper and lower quartiles of the

e the inbreeding effects that oc-
eak inbred animals that benefit
d to have lower mortality rates
eless, these results illustrate the
mortality rates in captive mam-
on in responses to inbreeding

reeding can be directly corre-
rvival and reproduction in cap-
. In populations without ped-
of the loss of heterozygosity is
ding depression in these popu-
es on the relationship between
itive relationship does exist, the
, genetic drift, or other factors
ness.
general, though not universal,
sity and various fitness compo-
rowth and developmental rate,

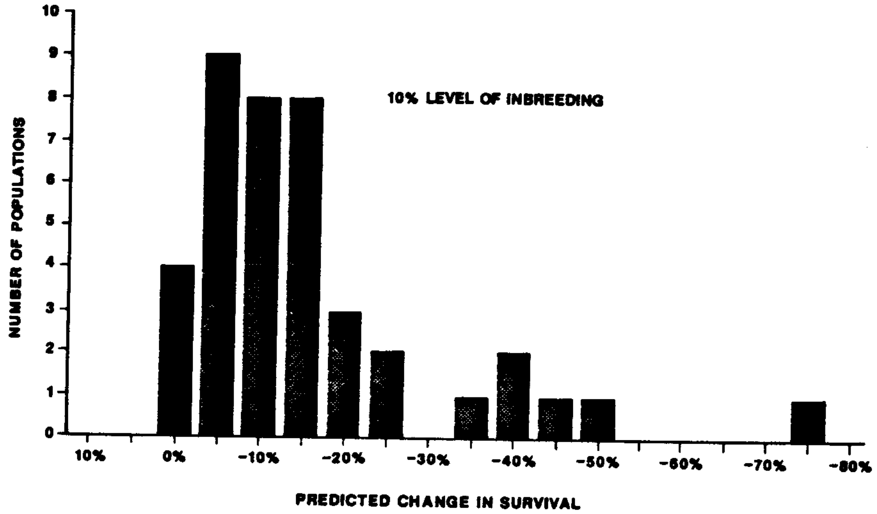


Figure 5.3. The predicted change in survival associated with an inbreeding level of 0.10 in 40 mammalian populations (Ralls et al. 1988).

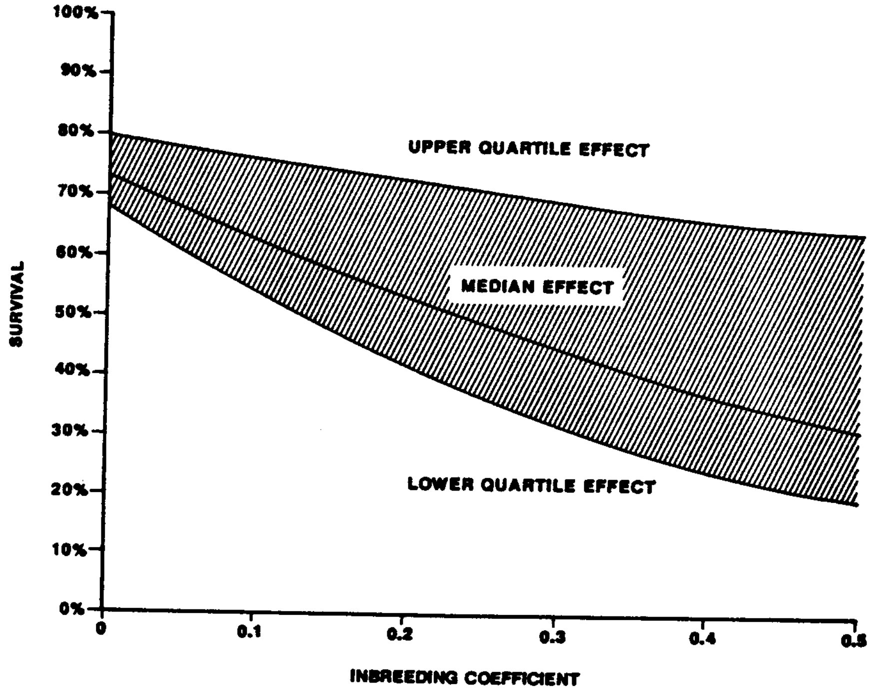


Figure 5.4. The predicted relationship between inbreeding and mortality in 40 mammalian populations (Ralls et al. 1988). The median, upper, and lower quartile effects of the distribution of 40 populations are shown.

reproductive rates, and developmental stability) in invertebrate and vertebrate populations (Allendorf and Leary 1986; Mitton and Grant 1984). Although Allendorf and Leary (1986,73) discuss several minor interpretational problems and complications common to many of these studies, they conclude that "there are many well-documented examples of advantages of heterozygotes in several components of fitness. There are fewer examples of disadvantages . . . Thus we conclude that, in general, there is a positive relationship between heterozygosity and fitness."

Inbreeding data from domestic animals and captive populations, as well as the evidence for a general relationship between heterozygosity and fitness, indicate that inbreeding and the loss of genetic diversity can have potentially disastrous effects on the survival of small populations near extinction. This can be illustrated for ferrets by observing the result of additional mortality due to inbreeding on estimates of black-footed ferret minimum viable population (MVP) sizes (Brussard and Gilpin, chap. 4, Harris et al., chap. 6, Gilpin and Soule 1986). Although the development of MVP estimates is beyond the scope of this chapter, a consideration in such estimates is the amount of time it takes a population of specified characteristics to go to extinction (MacArthur and Wilson 1967). A ferret population of effective size 5 will have an average 10% increase in inbreeding each generation. Data from captive populations (Fig. 5.4) show that the average increase in mortality associated with an inbreeding level of 10% is also 10%. Groves and Clark (1986) calculate times-to-extinction for black-footed ferret populations with carrying capacities of 40 and 50 (Table 5.1). This table conveniently illustrates the effects of increasing the death rates (*u*) in 10% increments. Times-to-extinction are reduced exponentially with each 0.10 increase in *u*, or each 10% increase in inbreeding.

Increased inbreeding and the decrease of heterozygosity, with its associated inbreeding depression, act to suppress population growth through a reduction in survivorship and fecundity. The reduction in growth and population size further increases the amount of inbreeding. Such an "inbreeding vortex" can easily drive an already small, fragile population to extinction (Gilpin and Soule 1986). Clearly, inbreeding and the loss of genetic diversity must be considered in the management of a captive breeding program for black-footed ferrets.

Two genetic mechanisms are involved in the reduction of fitness due to inbreeding. One is that as a population becomes increasingly inbred and more homozygous, deleterious recessive alleles are unmasked and expressed. The reduced fitness caused by the deleterious alleles is called "mutational load." The second mechanism is overdominance, or hetero-

---

Table 5.1. Eff
on the Time-to-
Ferret Populati

Carrying Capacity	Bi r
40	
50	

Source: Groves an
Note: The implic
to inbreeding on
be seen as an exp
death rates incre

zygote superiority. Heter
higher fitness than homoz
are called "heterotic" loci.
the frequency of heteroz
benefit. This type of redu
Both mutational and seg
pression, with the depres
perhaps the more impor

The severity of inbreed
mutational and segregati
tions clearly vary in the am
by the large variety of res
veyed by Ralls et al. (198

Populations with a prev
to carry less of a mutati
absence of genetic drift, s
reduce the mutational loa
ever, segregational load
fixed in populations that
tions accumulate both mu
levels of inbreeding depre
rally inbreeding populati
bottlenecks might be expe
sion when further inbred.

) in invertebrate and ver-
986; Mitton and Grant
73) discuss several minor
ommon to many of these
ll-documented examples
ponents of fitness. There
we conclude that, in gen-
terozygosity and fitness."
d captive populations, as
between heterozygosity
ss of genetic diversity can
ival of small populations
ts by observing the result
estimates of black-footed
es (Brussard and Gilpin,
ule 1986). Although the
scope of this chapter, a
of time it takes a popula-
inction (MacArthur and
ize 5 will have an average
ata from captive popula-
e in mortality associated
Groves and Clark (1986)
ferret populations with
This table conveniently
es (*u*) in 10% increments.
with each 0.10 increase

eterozygosity, with its as-
ress population growth
ndity. The reduction in
e amount of inbreeding.
an already small, fragile
86). Clearly, inbreeding
ered in the management
d ferrets.

reduction of fitness due
mes increasingly inbred
lleles are unmasked and
eleterious alleles is called
erdominance, or hetero-

Table 5.1. Effects of Increased Death Rates on the Time-to-Extinction in Black-Footed Ferret Populations

Carrying Capacity	Birth-rate	Death Rate	Time-to-Extinction
40	.5	.2	1.0×10^{15}
	.5	.3	3.0×10^{7}
	.5	.4	1.0×10^{3}
50	.5	.2	8.0×10^{18}
	.5	.3	5.0×10^{9}
	.5	.4	1.0×10^{4}

Source: Groves and Clark 1986.

Note: The implications of an additional 10% mortality due to inbreeding on the survival of the ferret populations can be seen as an exponential decline in the time-to-extinction as death rates increase.

zygote superiority. Heterozygous loci may, for a variety of reasons, have higher fitness than homozygous loci (Mitton and Grant 1984). Such loci are called "heterotic" loci. In inbred populations, there is a reduction in the frequency of heterozygous loci and a reduction in any associated benefit. This type of reduction in fitness is called "segregational load." Both mutational and segregational load contribute to inbreeding depression, with the depression associated with deleterious alleles being perhaps the more important of the two (Allendorf and Leary 1986).

The severity of inbreeding depression is a function of the amount of mutational and segregational load carried by that population. Populations clearly vary in the amount of load they carry (Fig. 5.2), as evidenced by the large variety of responses to inbreeding in the populations surveyed by Ralls et al. (1988).

Populations with a previous history of inbreeding might be expected to carry less of a mutational load than outbred populations. In the absence of genetic drift, selection against deleterious alleles will quickly reduce the mutational load with even slight levels of inbreeding. However, segregational load will be reduced at a slower rate and remain fixed in populations that become homozygous. Outbreeding populations accumulate both mutational and segregational load and have high levels of inbreeding depression when inbred. On the other hand, naturally inbreeding populations or populations that have passed through bottlenecks might be expected to have low levels of inbreeding depression when further inbred. The lack of inbreeding depression in populations that have a history of inbreeding is documented in domestic (Lasley 1978) and laboratory (Musialek 1980) animal populations, as well as in studies of human populations (Rao and Inbaraj 1980).

A viable approach to population management, therefore, might be to purge the genetic load from populations not previously exposed to inbreeding. Such a program, however, could have disastrous consequences on the survival of small, endangered populations.

The cost of successfully purging a population of its genetic load can be prohibitive. The increased mortality and reduced fecundity incurred during the process of exposing the mutational and segregational loads to selection in small, inbred lines are often severe enough to cause extinction. In efforts to produce successful inbred lines, Bowman and Falconer (1960) found that only 1 of 20 lines of mice survived intense inbreeding. The same results have been shown repeatedly in both laboratory populations (Lorenc 1980) and populations founded with wild-caught individuals (Lynch 1977; Soule 1980). The odds of successfully purging the genetic load from a single, small population of an endangered species are dangerously low.

Additionally, inbred lines that do survive are often less fit than their outbred counterparts. This is because the segregation load may remain in the inbred, homozygous population, even though the mutational load is absent. Reproduction and survival may be reduced, and the population may become much more susceptible to outbreaks of disease and environmental stochasticity. A case in point is the cheetah (*Acinonyx jubatus*). O'Brien et al. (1983, 1985) found that the cheetah has extremely low levels of genetic variation and suggested that the cheetah has had a history of small population size and is highly inbred. In addition, cheetahs are notoriously difficult to breed in captivity, have high levels of abnormal sperm, and appear to be highly sensitive to disease (O'Brien et al. 1985). The problem may be even more severe in very small populations subject to genetic drift. In small populations, genetic drift has more effect on changes in allele frequencies than does selection; and deleterious alleles, with their associated reduction in fitness, can become fixed in these small populations.

Intentional selection against deleterious alleles also drastically changes the genetic characteristics of the population. This domestication is clearly undesirable in populations intended for future release into natural habitats. The intentional purging of genetic load is indeed a risky option with certain undesirable results and should be carefully considered before being used in the management of endangered species (Hedrick et al. 1986).

It would seem, however,
inbreeding depression in n
tions with a history of sm
might be expected to be
degree to which a populatio
acting on a population an
population. Both selection
lations) are extremely diffi
often modeled using a varie
of a range of possible scen
Ralls et al. 1983). Additio
inbred populations or popu
variation show no depressi
electrophoretically detecta
ply total absence of geneti
teristics (Hedrick et al. 19
inbreeding, populations m
sion (recall the Swedish mi

The Père David's deer (*E*
attention of the West by
noticed this unusual deer
emperor. Extinct in the wi
captivity for as many as 3,0
David eventually managed
many is unknown, but pro
current population has de
Abbey, which itself was fou
pean population. Addition
II. The history of Père Davi
necks, and the species is bel
Foose and Foose 1983). I
(Ryder et al. 1981). Neverth
er mortality rates in inbred
young.

Additionally, even thoug
genetic variation (O'Brien
captive inbred cheetahs suf
than noninbred cheetahs (
of inbreeding and mortali
necessary to confirm this a

These data suggest that

documented in domestic
0) animal populations, as
) and Inbaraj 1980).
ent, therefore, might be to
ot previously exposed to
ld have disastrous conse-
l populations.
n of its genetic load can be
duced fecundity incurred
al and segregational loads
vere enough to cause ex-
bred lines, Bowman and
of mice survived intense
n repeatedly in both labo-
ations founded with wild-
. The odds of successfully
all population of an en-

re often less fit than their
regation load may remain
ough the mutational load
reduced, and the popula-
outbreaks of disease and
is the cheetah (*Acinonyx*
that the cheetah has ex-
ggested that the cheetah
is highly inbred. In addi-
ed in captivity, have high
ighly sensitive to disease
ven more severe in very
mall populations, genetic
quencies than does selec-
ated reduction in fitness,

alleles also drastically
ulation. This domestica-
ended for future release
f genetic load is indeed a
and should be carefully
nt of endangered species

It would seem, however, that one could safely ignore the threat of inbreeding depression in naturally inbreeding populations or populations with a history of small population size since these populations might be expected to be purged already of their genetic load. The degree to which a population is purged is a function of both the selection acting on a population and the degree and rate of inbreeding in the population. Both selection and the degree of inbreeding (in wild populations) are extremely difficult to estimate, as are their effects, and are often modeled using a variety of assumptions. The results are indicative of a range of possible scenarios (Lacy and Clark, chap. 7, this volume; Ralls et al. 1983). Additionally, it is not always true that historically inbred populations or populations with low levels of detectable isozyme variation show no depression with additional inbreeding. Absence of electrophoretically detectable protein variations does not necessarily imply total absence of genetic variation for adaptively important characteristics (Hedrick et al. 1986). Despite a history of domestication and inbreeding, populations may still be susceptible to inbreeding depression (recall the Swedish mink [Johansson 1961]).

The Père David's deer (*Elaphurus davidianus*) was first brought to the attention of the West by the missionary Father David, who in 1865 noticed this unusual deer in the hunting compound of the Chinese emperor. Extinct in the wild, Père David's deer had probably bred in captivity for as many as 3,000 years before being rediscovered. Father David eventually managed to send a few deer to Europe (exactly how many is unknown, but probably less than 5 lived to reproduce). The current population has descended from the captive herd at Woburn Abbey, which itself was founded by fewer than 18 deer from the European population. Additional bottlenecks occurred during World War II. The history of Père David's deer is characterized by a series of bottlenecks, and the species is believed to be highly inbred (Whitehead 1978; Foose and Foose 1983). Initial electrophoretic analysis confirms this (Ryder et al. 1981). Nevertheless, Foose (1983) found significantly higher mortality rates in inbred Père David's deer young than in noninbred young.

Additionally, even though the cheetah is almost completely lacking in genetic variation (O'Brien et al. 1983, 1985), initial results suggest that captive inbred cheetahs suffer from significantly higher mortality rates than noninbred cheetahs (O'Brien et al. 1985). A more detailed analysis of inbreeding and mortality patterns in both of these species will be necessary to confirm this association.

These data suggest that one should take care in making assumptions regarding the severity of inbreeding depression in populations with a history of small population size or low levels of genetic variation. It cannot automatically be assumed that inbreeding problems can be ignored in these populations.

The extant population of black-footed ferrets at Meeteetse is limited to approximately 3,000 hectares, and historical records indicate that the population has been both small (less than 100 animals) and probably genetically isolated since the 1930s (Clark et al. 1986; Lacy and Clark, chap. 7, this volume). Given a generation time of approximately 1.5 years, Lacy and Clark estimate that the Meeteetse population has been in a bottleneck for over 30 generations and could have lost between 16 and 73% of the variation present in the 1930s, which may itself have been very low. The historical bottleneck and the ensuing loss of variation have led several to suggest that the population has already been purged of its genetic load and that the genetic consequences of additional inbreeding can be ignored in developing captive-breeding plans (Pettus 1985).

Given the uncertainty of our assumptions regarding the historical events in the population and their effects, as well as the consequences of ignoring the potential impact of inbreeding depression, it seems that such advice is unsound. Consideration of the potential effects of inbreeding depression should be part of an integrated captive-breeding plan for black-footed ferrets.

Outbreeding Depression

A second consideration in developing a captive-breeding program for black-footed ferrets is the potential for outbreeding depression. Outbreeding depression can be defined as a reduction in fitness due to crossing individuals that are too distantly related. One type of outbreeding depression results from crossbreeding individuals from populations that have adapted to different local environments (local adaptation). Crossing individuals between these regions may then result in offspring fit for neither of the parents' habitats.

As an example of outbreeding depression due to local adaptation, Templeton et al. (1986) refer to translocation efforts with ibex. To supplement a previously introduced population of Tatra mountain ibex (*Capra ibex ibex*) in Czechoslovakia, bezoars (*C. i. aegrarus*) and Nubian ibex (*C. i. nubiana*) were imported from Turkey and the Sinai. Offspring of the subspecific hybrids were born in the dead of winter and could not survive. As a result, the population went extinct over several years (Greig 1979).

Outbreeding depressio
gene complexes. Coadapt
or karyotype complex ev
complexes or chromosom
genetic complexes are ada
local environments. An
found in the owl monkey
different chromosomal ra
improved when individua
in captivity (Cicmanec an
Templeton et al. (198
sibility of outbreeding pr
ferences between populat
ing problems. However,
result of coadaptation. In
strongly determined by g
drift rather than local ada
dence of gene-frequency
subject to genetic drift is
outbreeding depression.
future black-footed ferre
terpret any gene-frequen
Individuals can be gen
Such differences are pro
ing problems. Difference
suggestive of potential pr
lute indicators of an out
been found in populations
tions with considerable ge
outbreeding depression (
Outbreeding depressio
to a more limited extent, i
1986). Many studies on v
crossing (Cade 1983). H
mammals is scarce. Initial
outbreeding depression is
populations (Templeton a
to be more of a problem th
ic assays indicate otherwis
outbreeding depression.
The question of how im
complexes are to the futur

ssion in populations with a
els of genetic variation. It
eding problems can be ig-

rets at Meeteetse is limited
cal records indicate that the
100 animals) and probably
t al. 1986; Lacy and Clark,
time of approximately 1.5
etse population has been in
d have lost between 16 and
vhich may itself have been
suing loss of variation have
already been purged of its
es of additional inbreeding
ng plans (Pettus 1985).
ıs regarding the historical
well as the consequences of
depression, it seems that
he potential effects of in-
tegrated captive-breeding

ive-breeding program for
reeding depression. Out-
duction in fitness due to
ted. One type of outbreed-
lividuals from populations
ıments (local adaptation).
ay then result in offspring

ı due to local adaptation,
ion efforts with ibex. To
on of Tatra mountain ibex
. *i. aegrarus*) and Nubian
y and the Sinai. Offspring
ıd of winter and could not
xtinct over several years

Outbreeding depression can also result from disruption of coadapted gene complexes. Coadapted gene complexes can occur when a genetic or karyotype complex evolves or adapts in response to other genetic complexes or chromosomes. This differs from local adaptation in that genetic complexes are adapting to the state of other genes rather than to local environments. An example of karyotypic coadaptation can be found in the owl monkey (*Aotus trivirgatus*). Owl monkeys have several different chromosomal races (de Boer 1982), and reproductive fitness is improved when individuals with similar chromosome forms are paired in captivity (Cicmanec and Campbell 1977; Elliott et al. 1976).

Templeton et al. (1986) discuss techniques for predicting the possibility of outbreeding problems. Evidence of large gene-frequency differences between populations may be indicative of potential outbreeding problems. However, such differences may not necessarily be the result of coadaptation. In very small isolated populations, evolution is strongly determined by genetic drift, and differentiation may be due to drift rather than local adaptation or coadaptation due to selection. Evidence of gene-frequency differences between large populations not subject to genetic drift is of more weight in detecting the potential for outbreeding depression. Obviously the biogeography and history of any future black-footed ferret population will have to be examined to interpret any gene-frequency differences found.

Individuals can be genetically screened for karyotypic differences. Such differences are probably the best indicator of potential outbreeding problems. Differences in gene frequencies or karyotypes are only suggestive of potential problems and should not be interpreted as absolute indicators of an outbreeding effect. Outbreeding depression has been found in populations without detectable differences, while populations with considerable genetic differences have been found to have no outbreeding depression (Templeton et al. 1986).

Outbreeding depression has been found in plants, invertebrates, and, to a more limited extent, in vertebrate species (Shields 1982; Templeton 1986). Many studies on vertebrates indicate variable reactions to outcrossing (Cade 1983). However, evidence for outbreeding effects in mammals is scarce. Initial studies in captive populations indicate that outbreeding depression is not a contributing factor to mortality in these populations (Templeton and Read 1984). Inbreeding depression seems to be more of a problem than outbreeding depression and, unless genetic assays indicate otherwise, should be considered a higher priority than outbreeding depression.

The question of how important local adaptations and coadapted gene complexes are to the future management of the black-footed ferret is of interest only if other isolated populations of ferrets are found. Dispersal patterns of the ferrets suggest that different local adaptations or genetic coadaptation have probably not evolved within the Meeteetse population.

Management options for populations showing signs of inbreeding and outbreeding depression have been discussed in general terms elsewhere (Foose et al. 1986; Templeton et al. 1986; Templeton and Read 1984). Basically, outbreeding is a suggested management plan for populations likely to suffer from inbreeding depression. Similarly, populations likely to suffer from outbreeding depression should be managed as contained groups (Templeton et al. 1986).

These two recommendations are, in a sense, diametrically opposed in very small populations: avoiding inbreeding and maintaining genetic diversity necessitates outbreeding, while avoiding outbreeding necessitates population segregation and thus increased inbreeding. When managing small populations, we must therefore initially decide which strategy to adopt, since we cannot implement a management plan to avoid both outbreeding and inbreeding.

If the captive population of black-footed ferrets is founded solely from the Meeteetse population, as is now the case, it is unlikely that outbreeding depression will be a problem in the captive population. Although it is also possible that the population has been purged of its genetic load due to its history of moderate previous inbreeding (Lacy and Clark, chap. 7, this volume), conservative management practices dictate recognition of potential inbreeding effects.

Frankham et al. (1986) and Foose et al. (1986) discuss a variety of goals for the management of captive populations. Although the maintenance of genetic diversity is considered the most desirable goal for captive-breeding plans, they recognize the need to relax genetic considerations in favor of demographic considerations when the survival of the population is threatened. Certainly, this was the situation with the initial 18 black-footed ferrets in captivity. Strict emphasis should be placed on increasing the number of animals as rapidly as possible. This is necessary for both demographic reasons (small populations are more susceptible to extinction [Gilpin and Soule 1986]) and genetic reasons (the bottleneck effects of a founding event are minimized if postbottleneck population growth is rapid [Nei et al. 1975; Denniston 1978]). During this critical phase of growth, genetic considerations associated with maintaining genetic diversity (such as avoiding inbreeding and managing founder contribution [Foose et al. 1986]) must be secondary and should be considered only when the growth of the population is not compromised. When searching for reproductively compatible pairs,

however, pairings betwee
fore those between relate
During the critical phas
monitored. Records on s
data, parentage informa
for future analysis. As th
are available for breeding
genetic considerations. A
appropriate to begin eva
ever data have already b
population.
Various methods of ev
and reproduction are de
and Read 1984; Lee 198
will have been produced t
in detecting inbreeding e
statistically valid compar
rates. The concern is that
might conclude that the
difference is found, whe
to detect an effect. The p
proper conclusion.
Table 5.2 shows the
ferences between inbred
confidence (Lachin 1981
an inbreeding depressio
tality of 30% (inbred mo
(25 inbred and 25 noni
required if most births
course, the larger the in
detect it; and it is possible
to cause severe problems
its history.
If there are not enoug
that might be of concern
such an effect is slight,
continue to be managed
genetic diversity. Data on
monitored in either case.
to significantly affect m
If an inbreeding effect
affect the overall health

errets are found. Dispersal
ocal adaptations or genetic
l within the Meeteetse

wing signs of inbreeding
ssed in general terms else-
'86; Templeton and Read
anagement plan for popu-
ession. Similarly, popula-
ion should be managed as

, diametrically opposed in
and maintaining genetic
ling outbreeding necessi-
eased inbreeding. When
ore initially decide which
t a management plan to

ferrets is founded solely
e case, it is unlikely that
the captive population.
n has been purged of its
evious inbreeding (Lacy
e management practices
ects.

) discuss a variety of goals
though the maintenance
sirable goal for captive-
x genetic considerations
e survival of the popula-
ation with the initial 18
sis should be placed on
ossible. This is necessary
ns are more susceptible
enetic reasons (the bot-
nized if postbottleneck
nniston 1978]). During
rations associated with
inbreeding and manag-
must be secondary and
f the population is not
ively compatible pairs,

however, pairings between unrelated animals should be considered before those between related individuals.

During the critical phase, the effects of inbreeding should be carefully monitored. Records on successful and unsuccessful pairings, mortality data, parentage information, and other studbook data should be kept for future analysis. As the population becomes larger and more animals are available for breeding, there will be more flexibility in implementing genetic considerations. At this point (the "intensive care" phase), it is appropriate to begin evaluating the effects of inbreeding using whatever data have already been compiled during the critical phase of the population.

Various methods of evaluating the effects of inbreeding on mortality and reproduction are described elsewhere (Ralls et al. 1979; Templeton and Read 1984; Lee 1980). It is possible, however, that not enough data will have been produced to make a proper evaluation. A central problem in detecting inbreeding effects is the amount of data necessary to make a statistically valid comparison between inbred and noninbred mortality rates. The concern is that a negative result might be misinterpreted. One might conclude that there is no inbreeding effect if a nonsignificant difference is found, when, in fact, not enough data have been collected to detect an effect. The power of this test must be high enough to draw a proper conclusion.

Table 5.2 shows the sample sizes required to detect various differences between inbred and noninbred mortality rates with 90 and 95% confidence (Lachin 1981). For example, to be 90% certain of detecting an inbreeding depression of 40% relative to a baseline (noninbred) mortality of 30% (inbred mortality of 70%) requires a total sample size of 50 (25 inbred and 25 noninbred births). Even larger sample sizes will be required if most births are inbred, which is likely to be the case. Of course, the larger the inbreeding effect, the fewer data are needed to detect it; and it is possible that inbreeding effects of the magnitude likely to cause severe problems for a population will be easily detected early in its history.

If there are not enough data to detect the level of inbreeding effects that might be of concern to the population, or if data are available and such an effect is slight, then it is recommended that the population continue to be managed to enhance population growth and maintain genetic diversity. Data on the effects of inbreeding should continue to be monitored in either case. If an inbreeding effect becomes strong enough to significantly affect mortality patterns, it should be recognized soon.

If an inbreeding effect is detected and appears to be strong enough to affect the overall health and future chances of survival of a population,

Table 5.2. Sample Sizes Required to Detect Different Degrees of Inbreeding Depression

Inbred Mortality Rate	Noninbred (Base) Mortality Rate								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
	A: Sample required to detect a difference with 90% confidence								
0.1	—								
0.2	398	—							
0.3	126	639	—						
0.4	65	176	776	—					
0.5	40	83	202	844	—				
0.6	27	48	90	210	844	—			
0.7	19	30	50	90	202	776	—		
0.8	13	20	30	48	83	176	639	—	
0.9	9	13	19	27	41	68	133	433	—
1.0	6	9	12	16	22	30	45	73	159
	B: Sample required to detect a difference with 95% confidence								
0.1	—								
0.2	507	—							
0.3	159	806	—						
0.4	82	222	980	—					
0.5	50	104	254	1,066	—				
0.6	33	59	114	265	1,066	—			
0.7	23	37	62	114	254	980	—		
0.8	16	24	37	59	104	222	806	—	
0.9	11	16	23	34	51	85	168	547	—
1.0	7	10	14	19	27	38	56	92	200

Source: Lachin 1981.

Note: The sample sizes specified are the total number of births equally distributed between inbred and noninbred young required to detect a significant difference at the 0.05 level with a power of 0.90 (*A*) and 0.95 (*B*).

then a management plan to purge the population of its genetic load might be considered.

Templeton and Read (1984) discuss a management plan applied to a captive population of Speke's gazelle suffering from strong inbreeding depression. Their goal was to eliminate inbreeding depression by adapting the population to inbreeding. This was accomplished by selectively breeding healthy, inbred animals who would produce inbred offspring. Care was taken to avoid producing extremely inbred offspring as well as to choose parents that would maximize the genetic viability of the gene pool. Using the above management recommendations, they reduced the

---

genetic load in the popu
(Templeton and Read 19
ered for the black-foote
depression was found.

Implementing a plan
however, must be serious
tages. These are particul
mals to establish and sup
of the black-footed ferret
disadvantages seem negli
tion of the captive popula

Given the consequences
how severe does inbreedi
recommended? I recomm
severe enough to jeopard
This condition would exi
keep the population small
demographic fluctuations
cant declining trend tow
might be considered suffic
ing the population of its g

Once the levels of gene
could then revert back to
Read's (1984) results sug
genetic load relatively qui
rifying selection and m
considered.

Managing Inbreeding an

The possibility of discoveri
es some interesting questi
mals into a captive-breedi
genetic and demographic
founded captive populati
larger founder size will e
diversity, as well as increa
and rapid growth. Mergin
erozygosity, thereby resto
fitness in the offspring. If
outbreeding depression, th

ent Degrees of Inbreeding

tality Rate			
0.6	0.7	0.8	0.9
nce with 90% confidence			
—			
776	—		
176	639	—	
68	133	433	—
30	45	73	159
nce with 95% confidence			
—			
980	—		
222	806	—	
85	168	547	—
38	56	92	200

of births equally distributed
ı significant difference at the

.tion of its genetic load

ement plan applied to a
from strong inbreeding
ng depression by adapt-
ɔmplished by selectively
oduce inbred offspring.
ɔred offspring as well as
etic viability of the gene
ations, they reduced the

---

genetic load in the population by almost one-half in a 3-year period (Templeton and Read 1984). Such a management plan could be considered for the black-footed ferret population if significant inbreeding depression was found.

Implementing a plan to purge the population of its genetic load, however, must be seriously considered because of the severe disadvantages. These are particularly serious since release of captive-born animals to establish and supplement existing populations is a primary goal of the black-footed ferret recovery plan (Richardson et al. 1986). Such disadvantages seem negligible, however, if the alternative is the extinction of the captive population and possibly the entire species.

Given the consequences of implementing a plan to purge genetic load, how severe does inbreeding depression have to be before such a plan is recommended? I recommend that it be used only if the inbreeding is severe enough to jeopardize the continued survival of the population. This condition would exist if the depression was severe enough to: (a) keep the population small enough to remain dangerously susceptible to demographic fluctuations and catastrophic events, or (b) cause a significant declining trend towards extinction. Either of these conditions might be considered sufficient to implement a plan of reducing or purging the population of its genetic load.

Once the levels of genetic load are reduced, the management plan could then revert back to maintaining genetic diversity. Templeton and Read's (1984) results suggest that populations can be purged of their genetic load relatively quickly. In fact, a plan alternating between purifying selection and maintaining genetic diversity could also be considered.

Managing Inbreeding and Outbreeding Depression

The possibility of discovering other black-footed ferret populations raises some interesting questions regarding the incorporation of new animals into a captive-breeding program. There would be considerable genetic and demographic advantages in supplementing the Meeteetse-founded captive population with animals from other populations. A larger founder size will enhance the overall maintenance of genetic diversity, as well as increase the probability of successful reproduction and rapid growth. Merging the population could increase levels of heterozygosity, thereby restoring heterotic loci and promoting increased fitness in the offspring. If one chose to ignore the potential effect of outbreeding depression, the population should be initially merged and perhaps later subdivided, while maintaining limited gene flow (Foose et al. 1986).

Other populations that might be found will likely have been isolated from the Meeteetse population for many generations and may be fixed for alleles different from those in the Meeteetse population. It is possible that any fixed genetic difference will be due to genetic drift rather than selection. Under these conditions, the potential for outbreeding does exist and should be considered in the development of a breeding plan. However, inbreeding considerations should still take priority over outbreeding considerations.

If only a few individuals from another population are found, the primary goal will again be population growth, with the emphasis on choosing reproductively compatible pairings rather than genetically compatible pairings. However, a choice must first be made whether to search for reproductively compatible mates within or between populations. The karyotypes of the 2 populations should be compared. If differences are found, individuals within populations should be preferentially mated. If no differences exist, individuals between populations should be preferentially mated. As the population grows and there is more freedom in mate selection, the data can be analyzed for inbreeding and outbreeding effects using the methods described by Templeton and Read (1984). If inbreeding depression is a severe problem, preference should be given to outcrossing individuals rather than implementing a plan to purge the population of its genetic load. Likewise, if outbreeding depression is severe, plans should be developed to avoid pairings of individuals between populations (but also to avoid pairings between related individuals). If the data are inconclusive, then the population should be allowed to continue to grow. Pairings should be selected on the basis of maximizing genetic diversity. Test inbred and outbred crosses could be made if the population grows large enough so that animals become available. Additionally, if other large populations of ferrets are found, test pairings between populations could be conducted sooner.

If such pairings are compatible, a decision to merge the captive populations totally, partially, or not at all would have to be made. If inbreeding depression is absent, the best strategy might be to establish a third captive population by outcrossing some individuals from each of the 2 original populations, as suggested by Lacy and Clark (chap. 7, this volume).

This discussion of the potential outbreeding and inbreeding effects within and between future captive populations of black-footed ferrets should serve primarily to illustrate the types of management options

---

that might be con
acteristics of eithe
discovered black-
have to be based o
of the population

References

Allendorf, F. W., an
populations of ani
sity, ed. M. E. Soul
Bowman, J. C., and I
litter size in mice.
Buisman, A. K., an
Przewalski horses
lease into the wild,
Rotterdam: Foun
Horses.
Bulmer, M. G. 1973.
Cade, T. J. 1983. H
to conservation. I
S. M. Chambers, B
Benjamin-Cummi
Chai, C. K. 1969. Ef
Cicmanec, J. C., and
trivirgatus) in a lab
Clark, T. W., et al. 1
ferret environmen
Conway, W. G. 1980.
ed. M. E. Soule and
de Boer, L. E. M. 19
trivirgatus). *Interna*
Denniston, C. 1978. S
endangered specie
threatened species, ed
Press.
Dresser, B. 1984. Pro
endangered wildlif
Elliott, M. W., et al.
Anim. Sci. 26:1037-
Flesness, N. 1977. Ge
Yearbook 17:77–81.
Foose, T. J. 1983. T
of biotic diversity.

nited gene flow (Foose et

likely have been isolated
rations and may be fixed
population. It is possible
genetic drift rather than
al for outbreeding does
nent of a breeding plan.
ill take priority over out-

pulation are found, the
ı, with the emphasis on
rather than genetically
irst be made whether to
thin or between popula-
hould be compared. If
lations should be prefer-
als between populations
ition grows and there is
analyzed for inbreeding
ribed by Templeton and
re problem, preference
er than implementing a
Likewise, if outbreeding
ed to avoid pairings of
avoid pairings between
ve, then the population
s should be selected on
st inbred and outbred
s large enough so that
er large populations of
ions could be conducted

merge the captive popu-
to be made. If inbreed-
t be to establish a third
uals from each of the 2
d Clark (chap. 7, this

and inbreeding effects
of black-footed ferrets
f management options

that might be considered. Obviously, it is impossible to predict the characteristics of either the future captive population or any other yet-to-be-discovered black-footed ferret populations. Management decisions will have to be based on the specific genetic and demographic characteristics of the populations present at that time.

References

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. In *Conservation biology: The science of scarcity and diversity,* ed. M. E. Soule, 57–76. Sunderland, Mass.: Sinauer Assoc.

Bowman, J. C., and D. S. Falconer. 1960. Inbreeding depression and heterosis of litter size in mice. *Genet. Res. Camb.* 1:262–74.

Buisman, A. K., and R. van Weeren. 1982. Breeding and management of Przewalski horses in captivity. In *Breeding Przewalski horses in captivity for release into the wild,* ed. J. Bouman, I. Bouman, and A. Groeneveld, 76–111. Rotterdam: Foundation for the Preservation and Protection of Przewalski Horses.

Bulmer, M. G. 1973. Inbreeding in the great tit. *Hereditas* 30:313–25.

Cade, T. J. 1983. Hybridization and gene exchange among birds in relation to conservation. In *Genetics and conservation.* ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, 288–309. Menlo Park, Calif.: Benjamin-Cummings.

Chai, C. K. 1969. Effects of inbreeding in rabbits. *J. Hered.* 60:64–70.

Cicmanec, J. C., and A. K. Campbell. 1977. Breeding the owl monkey (*Aotus trivirgatus*) in a laboratory environment. *Lab. Anim. Sci.* 27:512–17.

Clark, T. W., et al. 1986. Description and history of the Meeteetse black-footed ferret environment. *Great Basin Nat. Memoirs* 8:72–84.

Conway, W. G. 1980. An overview of captive propagation. In *Conservation biology,* ed. M. E. Soule and B. A. Wilcox, 199–208. Sunderland, Mass.: Sinauer Assoc.

de Boer, L. E. M. 1982. Karyological problems in breeding owl monkeys (*Aotus trivirgatus*). *Internat. Zoo Yearbook* 22:119–24.

Denniston, C. 1978. Small population size and genetic diversity: Implications for endangered species. In *Endangered birds: Management techniques for preserving threatened species,* ed. S. A. Temple, 281–89. Madison, Wis.: Univ. of Wisconsin Press.

Dresser, B. 1984. Proceedings of the conference on reproductive strategies for endangered wildlife. *Zoo Biol.* 3:307–9.

Elliott, M. W., et al. 1976. Management and breeding of *Aotus trivirgatus. Lab. Anim. Sci.* 26:1037–40.

Flesness, N. 1977. Gene pool conservation and computer analysis. *Internat. Zoo Yearbook* 17:77–81.

Foose, T. J. 1983. The relevance of captive propagation to the conservation of biotic diversity. In *Genetics and conservation,* ed. C. M. Schonewald-Cox,

S. M. Chambers, B. MacBryde, and L. Thomas, 374–401. Menlo Park, Calif.: Benjamin-Cummings.

Foose, T. J., and E. Foose. 1983. Demographic and genetic status and management. In *The biology and management of an extinct species: Père David's deer,* ed. B. B. Beck and C. Wemmer, 133–86. Park Ridge, N.J.: Noyes.

Foose, T. J., et al. 1986. Propagation plans. In *Proc. workshop genetic management of captive populations,* ed. K. Ralls and J. D. Ballou. *Zoo Biol.* 5:139–46.

Forrest, S. C., et al. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985. *J. Mammal.* 69:261–73.

Frankham, R., et al. 1986. Selection in captive populations. In *Proc. workshop genetic management of captive populations,* ed. K. Ralls and J. D. Ballou. *Zoo Biol.* 5:127–38.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: Processes of species extinction. In *Conservation biology: The science of scarcity and diversity,* ed. M. E. Soule, 19–34. Sunderland, Mass.: Sinauer Assoc.

Greig, J. C. 1979. Principles of genetic conservation in relation to wildlife management in Southern Africa. *South African J. Wildl. Res.* 9:57–78.

Groves, C. R., and T. W. Clark. 1986. Determining minimum population size for recovery of the black-footed ferret. *Great Basin Nat. Memoirs* 89:150–59.

Hedrick, P. W., et al. 1986. Protein variation, fitness and captive propagation. In *Proc. workshop genetic management of captive populations,* ed. K. Ralls and J. D. Ballou. *Zoo Biol.* 5:91–99.

Johansson, I. 1961. Studies on the genetics of ranch bred mink. I. The results of an inbreeding experiment. *Z. Tierzuecht. Zuechtungs-Biol.* 72:293–97.

Lachin, J. M. 1981. Introduction to sample size determination and power analysis for clinical trials. *Controlled Clinical Trials* 2:93–113.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection and population subdivision. *Conserv. Biol.* 1:143–58.

Lasley, J. F. 1978. *Genetics of livestock improvement.* Englewood Cliffs, N.J.: Prentice-Hall.

Lee, E. T. 1980. *Statistical methods for survival data analysis.* Belmont, Cal.: Lifetime Learning Pubns.

Lorenc, E. 1980. Analysis of fertility in inbred lines of mice derived from populations differing in their genetic load. *Zeierzeta Laboratoryjne* 17:3–16.

Lynch, C. B. 1977. Inbreeding effects upon animals derived from wild populations of *Mus musculus. Evolution* 31:525–37.

MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography.* Princeton, N.J.: Princeton Univ. Press.

McPhee, H. C., et al. 1931. An inbreeding experiment with Poland China swine. *J. Hered.* 22:383–403.

Martin, R. D. 1975. *Breeding endangered species in captivity.* London: Academic Press.

Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Ann. Rev. Ecology and Syst.* 15:479–500.

Morton, N. E., et al. 1956
data on consanguineou

Musialek, B. 1980. Effect
Genetica Polonica 21:46

Nei, M., et al. 1975. The b
Evolution 29:1–10.

O'Brien, S. J., et al. 198
Science 221:459–62.

O'Brien, S. J., et al. 1985.
Science 227:1428–34.

Packer, C. 1979. Inter-trc
Anim. Behav. 27:1–36.

Pettus, D. 1985. Genetic
proceedings, Wyoming Ga
Cheyenne, Wyo.: Wyor

Ralls, K. and J. D. Ballou
conservation. ed. C. M. S
Thomas, 164–84. Men

Ralls, K., et al. 1983. Gen
siderations and manag

Ralls, K., et al. 1979. Inbr
ungulates. *Science* 206:

Ralls, K., J. Ballou, and A
and the cost of inbreed

Rao, P. S. S., and S. G. I
development. *J. Med. G*

Richardson, L., et al. 198
options and considerat

Roberts, M. 1982. Demog
(*Ailurus fulgens*). *Zoo Bi*

Ryder, O. A., et al. 1981.
Evolution Today, ed. G.
Carnegie-Mellon Univ.

Shields, W. M. 1982. *Phil*
State Univ. of New Yo

Shoemaker, A. H. 1982. T
tion of pedigree leopar

Soule, M. E. 1980. Thresh
potential. In *Conservati*
Soule and B. A. Wilcox

Templeton, A. R. 1979. T
ic revolutions and th
strains. *Genetics* 92:128

Templeton, A. R. 1986. C
tion biology: The science
derland, Mass.: Sinaue

-401. Menlo Park, Calif.:
ietic status and manage-
: Père David's deer, ed. B.
: Noyes.
hop genetic management of
Biol. 5:139–46.
lack-footed ferret (Mus-
Mammal. 69:261–73.
ations. In *Proc. workshop*
nd J. D. Ballou. *Zoo Biol.*
opulations: Processes of
scarcity and diversity, ed.
oc.
elation to wildlife man-
es. 9:57–78.
num population size for
Memoirs 89:150–59.
captive propagation. In
, ed. K. Ralls and J. D.
mink. I. The results of
iol. 72:293–97.
ation and power analy-
l populations: interact-
nd population subdivi-
vood Cliffs, N.J.: Pren-
s. Belmont, Cal.: Life-
derived from popula-
yne 17:3–16.
ved from wild popula-
of island biogeography.
h Poland China swine.
y. London: Academic
rotein heterozygosity,
Rev. Ecology and Syst.

Morton, N. E., et al. 1956. An estimate of the mutational damage in man from data on consanguineous marriages. *Proc. Nat. Acad. of Sci.* 42:855–63.

Musialek, B. 1980. Effect of the population size on decrease of fertility in mice. *Genetica Polonica* 21:461–75.

Nei, M., et al. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1–10.

O'Brien, S. J., et al. 1983. The cheetah is depauperate in genetic variation. *Science* 221:459–62.

O'Brien, S. J., et al. 1985. Genetic basis for species vulnerability in the cheetah. *Science* 227:1428–34.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis. Anim. Behav.* 27:1–36.

Pettus, D. 1985. Genetics of small populations. In *Black-footed ferret workshop proceedings, Wyoming Game Dept.*, ed. S. Anderson and D. Inkley, 22.1–22.11. Cheyenne, Wyo.: Wyoming Fish and Game Dept.

Ralls, K. and J. D. Ballou. 1983. Extinction: Lessons from zoos. In *Genetics and conservation*. ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, 164–84. Menlo Park, Calif.: Benjamin-Cummings.

Ralls, K., et al. 1983. Genetic diversity in California sea otters: Theoretical considerations and management implications. *Biol. Conserv.* 25:209–32.

Ralls, K., et al. 1979. Inbreeding and juvenile mortality in small populations of ungulates. *Science* 206:1101–3.

Ralls, K., J. Ballou, and A. R. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* 2:185–93.

Rao, P. S. S., and S. G. Inbaraj. 1980. Inbreeding effects on fetal growth and development. *J. Med. Genet.* 17:27–33.

Richardson, L., et al. 1986. Black-footed ferret recovery: A discussion of some options and considerations. *Great Basin Nat. Memoirs* 8:169–84.

Roberts, M. 1982. Demographic trends in a captive population of red pandas (*Ailurus fulgens*). *Zoo Biol.* 1:119–26.

Ryder, O. A., et al. 1981. Monitoring genetic variation in endangered species. In *Evolution Today*, ed. G. G. E. Scudder and J. L. Reveal, 417–24. Pittsburgh: Carnegie-Mellon Univ.

Shields, W. M. 1982. *Philopatry, inbreeding and the evolution of sex.* Albany, N.Y.: State Univ. of New York.

Shoemaker, A. H. 1982. The effect of inbreeding and management on propagation of pedigree leopards. *Internat. Zoo Yearbook* 22:198–206.

Soule, M. E. 1980. Thresholds for survival: Maintaining fitness and evolutionary potential. In *Conservation biology: An evolutionary-ecological perspective*, ed. M. E. Soule and B. A. Wilcox, 151–69. Sunderland, Mass.: Sinauer Assoc.

Templeton, A. R. 1979. The unit of selection in *Drosophila mercatorum*. II. Genetic revolutions and the origin of coadapted genomes in parthenogenetic strains. *Genetics* 92:1283–93.

Templeton, A. R. 1986. Coadaptation and outbreeding depression. In *Conservation biology: The science of scarcity and diversity*. ed. M. E. Soule, 19–34. Sunderland, Mass.: Sinauer Assoc.

Templeton, A. R., and B. Read. 1983. The elimination of inbreeding depression in a captive herd of Speke's gazelle. In *Genetics and conservation.* ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, 241–61. Menlo Park, Calif.: Benjamin-Cummings.

———. 1984. Factors eliminating inbreeding depression in a captive herd of Speke's gazelle. *Zoo Biol.* 3:177–99.

Templeton, A. R., et al. 1986. Local adaptation, coadaptation and population boundaries. *Zoo Biol.* 5:115–25.

Whitehead, G. K. 1978. *Threatened deer.* Morges, Switzerland: IUCN Publ.

Wildt, D. E., et al. 1982. Influence of inbreeding on reproductive performance, ejaculate quality and testicular volume in the dog. *Theriogen.* 17:445–51.

Wright, S. 1922. The effects of inbreeding and crossbreeding on guinea pigs. I. Decline in vigor. *Bull. U.S. Dept. Agriculture* 1093:37–63.

———. 1977. *Evolution and the genetics of populations,* Vol. 3. Chicago, Ill.: Univ. of Chicago Press.

Young, C. L., et al. 1969. Inbreeding investigations with diary cattle in the north central region of the United States. *Minn. Univ. Agricul. Exper. Stat. Tech. Bull.* 266:3–15.

6

RICHARD B. HAR

AND MARK L. SHA

Extinction Proba
Black-Footed Fe

Black-footed ferrets, on
day critically endangere
isolates that are vulnera
from demographic, env
the species to healthy n
protection, but also kno
for isolated ferret popu
tinction probabilities, re

The use of stochastic s
populations was initially
cess is roughly analogou
apply appropriate stocha
attempt to determine th
occur with acceptably lo
simulation to the problen
estimating probabilities
demographic and enviro
the absence of 1 of the 2
population viability beca
Clark [1986] and Lacy an

Support for this work was pr
Department of Fish, Wildlife a
and the New York Zoological
support came from the Monta
Montana Computing Center, an
tions were performed on the DE
sity of Montana. We thank L. Gi
State University of New York,
program. We also appreciate th