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# Conservation Implications of the Natural Loss of Lineages in Wild Mammals and Birds

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**Abstract:** *Because populations in zoological parks and nature reserves often are derived from only a few individuals, conservationists have attempted to minimize founder effects by equalizing family group sizes and increasing the reproductive contributions of all individuals. Although such programs reduce potential losses of genetic diversity, information is rarely available about the actual persistence of family groups or genetic lineages in natural populations. In the absence of such data, it can be difficult to weigh the importance of human intervention in the conservation of small populations. Separate long-term studies of two mammals, the North American bison (*Bison bison*) and the white-nosed coati (*Nasua narica*), and a bird, the Acorn Woodpecker (*Melanerpes formicivorus*), demonstrate differential extinction of genetic lineages. Irrespective of the mechanisms affecting population structure, which may range from stochastic environmental events to such behavioral phenomena as poor intrasexual competitive abilities, our results show that lineages can be lost at rapid rates from natural populations. A survey of comparable studies from the literature indicates that the loss of matriline over the course of the study varies from 3% to 87% in wild mammals and from 30% to 80% in birds, with several small mammals losing approximately 20% of matriline per year of study. These lineage extinctions were not an artifact of the length of the study or the generation time of the species. Such rapid losses of lineages in less than 20-year periods in natural populations suggest that efforts to maintain maximal genetic diversity within populations may not always reflect processes that occur in the wild. Conservation biologists need to give further thought to the extent to which parity among genetic lines should be a primary goal of management of captive and small wild populations.*

## Implicaciones de la Conservación en la Pérdida Natural de Linajes en Mamíferos y Aves Silvestres

**Resumen:** *Debido a que las poblaciones en los parques zoológicos y reservas naturales frecuentemente se derivan de sólo unos pocos individuos, los conservacionistas han intentado minimizar los efectos causado por el efecto fundador igualando los tamaños de los grupos familiares e incrementando las contribuciones reproductivas de todos los individuos. Tales programas reducen las pérdidas potenciales de diversidad genética, sin embargo rara vez hay información disponible sobre la persistencia real de los grupos familiares o linajes genéticos en las poblaciones naturales. Dada la ausencia de tales datos, puede ser difícil contrapesar los argumentos sobre la importancia de la intervención humana en la conservación de poblaciones pequeñas. Estudios a largo plazo con dos mamíferos, el bisonte norteamericano (*Bison bison*) y el coati de nariz blanca (*Nasua narica*), y uno con el pájaro carpintero de bellota (*Melanerpes formicivorus*), demuestran independientemente la extinción diferencial de linajes genéticos. Independientemente de los mecanismos que afectan a la estructura de las poblaciones, los cuales pueden variar desde eventos ambientales al azar hasta fenómenos de conducta tales como capacidades competitivas intrasexuales inadecuadas, nuestros resultados demuestran que los linajes pueden desaparecer de las poblaciones naturales en ritmos acelerados. Una revisión de publicaciones sobre investigaciones semejantes muestra una pérdida de líneas maternas a lo largo del estudio que varía del 3 al 87% en mamíferos silvestres y del 30 al 80% en aves. En varios micromamíferos se han detectado pérdidas de aproximadamente el 20% de las líneas maternas por año de estudio. Estas extinciones de linajes no fueron un artefacto de la duración del estudio ni de la duración de la generación de la especie.*

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*Tales pérdidas rápidas de linajes en períodos de menos de 20 años en las poblaciones naturales sugieren la posibilidad de que los esfuerzos de mantener la diversidad genética máxima dentro de las poblaciones no siempre reflejan los procesos que ocurren en la naturaleza. Los biólogos conservacionistas necesitan reflexionar más a fondo sobre hasta qué grado la paridad entre linajes genéticos debe ser una meta primordial de la administración de animales en cautiverio y de pequeñas poblaciones silvestres.*

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## Introduction

A fundamental challenge awaiting future conservation biologists is the development of management tactics to simulate the genetic processes that occur in undisturbed populations. Although knowledge of these processes is only now emerging for free-living higher vertebrates (Chepko-Sade & Halpin 1987; Clutton-Brock 1988; Grant & Grant 1989; Partridge 1989; Hoezel et al. 1993; Avise & Hamrick 1995), a strategy of prudence is already being practiced in most zoological parks. To ensure retention of genetic diversity, most captive breeding programs attempt to equalize reproductive success as much as possible among all members of the current population. This effort has two goals. First, an immediate goal is to maximize heterozygosity and minimize the breeding of individuals homozygous for deleterious alleles, thereby retaining the vigor and genetic diversity of the captive population (Foote & Ballou 1988; Ashworth & Parkin 1992). Second, a long-term goal is to maximize genetic diversity of the captive population whose progeny may someday be returned to the wild either to enhance existing populations or to establish new populations (Kleiman 1989; Haig et al. 1990, 1994; Rave et al. 1994; Ballou et al. 1995). Similarly, wildlife biologists often translocate animals between wild populations to increase genetic variation and effective population sizes, hoping thereby to increase the long-term survival probabilities of wild populations (Griffith et al. 1989; Burke 1991; Dodd & Seigel 1991; Haig et al. 1993; Smith & Clark 1994).

Nonetheless, efforts to minimize immediate genetic losses may be insufficient to assure the long-term maintenance of uncommon alleles (Crow & Kimura 1970; Wright 1978; Fuerst & Maruyama 1986; Ballou 1991), and only rarely has information been available about the actual persistence of family groups or genetic lineages in natural populations (Simberloff 1988). Such information is critical to gain a fuller understanding of genetic population structure and the extent to which unforeseen and unpredictable events may shape that structure. For instance, the 75–125 lions (*Panthera leo*) that currently inhabit the Ngorongoro Crater in Tanzania are descendants of only 15 survivors of a biting-fly epizootic nearly 30 years ago (Packer et al. 1991b), and the entire Isle Royale wolf (*Canis lupus*) population derives from a single female (Wayne et al. 1991). Similarly, about 80% of all new breeding adults in a population of Florida Scrub

Jays (*Apelocoma coerulescens coerulescens*) were produced in only 5 of 13 years of the study, reflecting high variability in between-year reproductive success (Fitzpatrick & Woolfenden 1988). Nevertheless, without further information on the extent of allelic or genetic lineage change in populations free from human disturbance, it will remain difficult to develop a rational approach to the long-term conservation of populations and their genetic population structure.

Because of the importance of natural lineage loss to both theoretical conservation biology and the practical management of threatened populations, we attempted to estimate patterns and frequencies of lineage loss in free-living populations. First, we explored possible variables that govern lineage turnover within populations using detailed demographic, behavioral, and reproductive data from our own longitudinal studies of North American bison (*Bison bison*), white-nosed coatis (*Nasua narica*), and Acorn Woodpeckers (*Melanerpes formicivorus*). Second, we broadened the scope of our analysis by presenting estimates from the literature of the loss of lineages (matrilines or patriline) from population studies of other taxa of mammals and birds, data critical to the development of baseline information on this issue. Third, we summarized some factors likely to affect lineage loss in natural populations, and, while recognizing that it is unlikely that similar factors will lead to similar lineage loss pressures in different taxonomic groups, we attempted to address the importance of this issue for future conservation efforts.

In considering this problem, we make several caveats. None of these studies was designed specifically to examine the actual loss of genetic alleles, and each necessarily used different methods to define and address lineage loss. For bison, lineage loss was measured in terms of variance in the mating success of individuals from mixed lineages known to have no recent ties in a demographic restoration effort. For coatis, lineage loss was assessed in terms of the extinction of female-bonded social groups. Among mammal species social groups can often be equated with genetic lineages because strict philopatry of one sex, usually females, generally results in sympatric, unrelated family groups or matriline (Greenwood 1980; Packer et al. 1991a; Melnick & Hoelzer 1992; Waser 1996; for coatis, Gompper 1994). For Acorn Woodpeckers we assessed the variance of reproductive success of individuals as well as the persistence of family

lineages. Our cross-species analyses were similarly varied as to how lineage loss was estimated. Nonetheless, we hope this essay will provoke researchers working with captive populations to assess the likelihood of rapid lineage loss following reintroduction to the wild and that it will provoke field researchers to look for and report rates of lineage loss for wild populations.

## The Studies

### North American Bison

Bison are the largest terrestrial species in North America and at one time numbered 30–60 million individuals. Today, most bison are found in small, heavily managed populations. The bison data presented here stem from more than 8750 hours of observation of animals in the 250-km<sup>2</sup> Sage Creek Wilderness Area of Badlands National Park, South Dakota (USA) by JB and co-workers from 1985 to 1989 (Berger & Cunningham 1994). Bison were reintroduced to the Badlands in 1963, and the population grew at a rate of about 11% per year until the early 1970s. The population was controlled by removal of animals until the commencement of this study, when it grew from approximately 300 to 775 individuals in 1989. A proportion of this expanding population was transplanted to the neighboring Pine Ridge Indian Reservation in 1989.

The Badlands population contains two sympatric lineages of known ancestry, one derived exclusively from three founders from Denver, Colorado (CL line) in 1925 and the other from six founders from Fort Niobrara National Wildlife Refuge, Nebraska (NL line) in 1913. The lines were allopatric until 1984, when the CL was introduced into Badlands; the NL had been there since 1963 (McClenaghan et al. 1990). The lineages differ phenotypically, CL individuals are smaller and darker (Berger & Peacock 1988). Body weights, ages, skeletal dimensions, and growth and reproductive rate of animals from both lines were known from capture, immobilization, or estimation with a photogrammetric caliper (Berger & Cunningham 1988, 1994; Berger 1989, 1992). The information reported here on variance in reproductive success is based upon observations of 261 copulations (Berger & Cunningham 1991).

### White-nosed Coatis

White-nosed coatis are 4–6 kg omnivores with a social structure unique within the order Carnivora. Several adult females and their immature offspring form permanent social groups, referred to as bands, of up to 30 individuals. These bands are not harems; rather, all adult males are solitary except during a brief synchronous mating season (Kaufmann 1962; Gompper 1995).

MEG has been studying the white-nosed coati on Barro Colorado Island, Panama, since 1989. Barro Colorado is a 16-km<sup>2</sup> island of lowland tropical moist forest (Croat 1978) located in freshwater Lake Gatun, an artificial body of water created when the Chagras River was dammed to form the Panama Canal. The island is separated from the mainland by 200–1000 m, and coatis have been observed swimming in the lake, indicating incomplete isolation of the population. Wet and dry seasons produce contrasting seasons of food availability which limit Barro Colorado's mammal populations (Smythe 1970; Foster 1982a; Leigh & Windsor 1982; Smythe et al. 1982). In addition, poor fruiting seasons occur occasionally, which may lead to large-scale die-offs in the populations of many frugivores, including coatis (Foster, 1982b). Most individuals from six bands were captured and marked or were recognizable from natural markings. Additional details on the study population and methodology are given in Gompper (1994, 1997).

Between 1987 and 1993 the population density of coatis on Barro Colorado was 48.2–55.6 individuals/km<sup>2</sup>, mean ( $\pm$  SD) group size was  $15.3 \pm 6.1$  individuals, and mean foraging group size was  $7.2 \pm 2.8$  individuals (Gompper 1994, 1997; Wright et al. 1994). In 1992 an El Niño weather pattern induced a 1993 fruit failure for many tree species fed on by coatis, and the population declined sharply in 1994 (MEG, unpublished data).

### Acorn Woodpeckers

Acorn Woodpeckers are cooperative breeders and live in permanently territorial social groups containing both breeders and nonreproductive helpers. Most groups construct storage trees or graneries in which large numbers of acorns are stored as a winter food source. The number of storage facilities present on a territory has a major influence on the reproductive success and survivorship of individuals living on that territory (Stacey & Ligon 1987).

PBS and co-workers studied Acorn Woodpeckers in Water Canyon, located approximately 30 km west of Socorro, New Mexico, in the Magdalena Mountains. The site is riparian canyon bottom and pine-oak woodland. The study population consisted of 18–35 groups (mean group size  $\pm$  SD =  $2.6 \pm 0.9$  individuals; range = 2–5) and was isolated from other populations by large areas of unsuitable habitat. Individual birds were marked with unique combinations of color bands, and all breeding attempts were determined for each group each year. The data reported here cover the 10-year period from 1975–1984. Additional details of the study population and methodology are given by Stacey (1979) and Stacey and Ligon (1987, 1991).

### Other Mammals

Data on other mammals were taken from long-term field studies (Table 1). For each study we determined the length of the study and the percentage of lineages retained over

the study period. When it was not reported in the original field study, we obtained additional life-history information on body size and generation time from Armitage (1981), Eisenberg (1981), Gittleman (1986), Albon et al. (1983), and Costa et al. (1986). Body size has an important influence on turnover rates in mammals (Clutton-Brock & Harvey 1983), especially in long-lived species studied for only a portion of their generation times. But because generation times can best be approximated by data from life tables in stationary populations (Caughley 1977; Pianka 1988), data that often do not exist, we approximated generation time by examining age of first reproduction. Although this parameter underestimates true generation time in animals that breed repeatedly, it is appropriate here because it allows examination of lineage loss while assuming a maximum potential for turnover—the greatest number of possible generations for each study.

We analyzed these data in two ways. First, linear and logistic regression were used to examine relationships involving the percentage of lineages retained. This dependent variable is bounded between 0 and 1 and was therefore transformed by means of the formula

$$\text{logit}(y) = \log((y/100)/(1 - (y/100)))$$

A linear regression line was fitted between logit(*y*) and the independent variables to identify correlation coefficients and significance values. Second, we attempted to correct for possible phylogenetic nonindependence in the data set (Harvey & Pagel 1991). A robust comparative analysis incorporating recent mammalian phylogenies could not be done because representation of data from different families was generally sparse (15 species in six orders) and because higher-level mammalian phylogenies are poorly resolved and controversial. But we attempted to circumvent this problem somewhat by repeating the analysis at the levels of family and order (Harvey & Pagel 1991), thereby avoiding a bias toward taxa that are rich in data. Mean values for higher taxa were calculated by averaging species values within genera, genera within families, and families within orders.

Results and Discussion

Breeding Disparity and Lineage Loss among Bison

We begin by considering whether one bison lineage was reproductively more successful than the other. Three

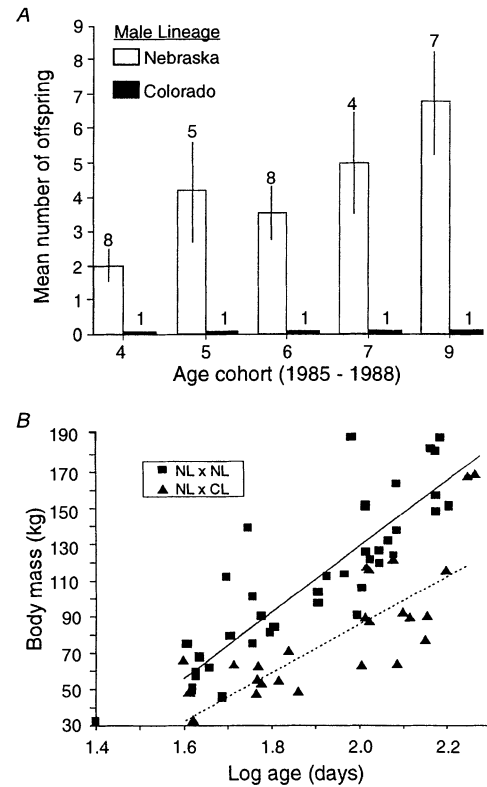
Table 1. The percentage of lineages lost during the study period and life-history traits for mammalian species.\*

Species	Study period (years)	Lineages retained (%)	Mean female mass (kg)	Age of first reproduction (years)	Reference
Red deer <i>Cervus elephus</i>	17	97	33	2	Clutton-Brock et al. 1988
Feral horse <i>Equus caballus</i>	6	92	435	2.1	Berger 1986; J. Berger unpublished data
Toque macaque <i>Macaca sinica</i>	16	75	3.4	4	Dittus 1986
Yellow baboon <i>Papio cynocephalus</i>	18	63.6	12.98	5.5	Altmann 1980; J. Altman personal communication
African lion <i>Panthera leo</i>	13	96	135.5	4.4	Packer et al. 1988
African wild dog <i>Lycaon pictus</i>	12	60	22.2	3.1	Frame et al. 1979
Black bear <i>Ursus americanus</i>	23	92	97	5.0	Rogers 1987; L. Rogers personal communication
White-nosed coati <i>Nasua narica</i>	7	60	3.7	2.0	Gompper 1994, 1997; M. Gompper unpublished data
European badger <i>Meles meles</i>	5	87.5	10.9	1.4	Kruuk & Parish 1987
Elephant seal <i>Mirounga angustirostris</i>	21	93	568	3.5	Le Bouef & Reiter 1988; B. Le Bouef personal communication
Bush hyrax <i>Heterohyrax brucei</i>	6	46	1.8	2.7	Hoeck 1982
Plains viscacha <i>Lagostomus maximus</i>	5	12.5	3.0	0.7	Branch 1989; L. Branch personal communication
Thirteen-lined squirrel <i>Spermophilus tridecemlineatus</i>	4	20	0.11	1	McCarley 1970
Richardson's ground squirrel <i>Spermophilus richardsoni</i>	4	20	.23	1	Michener 1980
Yellow-bellied marmot <i>Marmota flaviventris</i>	23	13	2.56	2	Armitage 1984; 1987

\*African wild dogs males are the philopatric sex, whereas both sexes disperse in horses; for other species females are the philopatric sex.

life-history traits were examined: offspring production, juvenile mortality, and variation in male reproductive (copulatory) success (Berger & Cunningham 1994). Neither annual juvenile mortality ( $\chi^2 = 0.005$ ;  $n = 236$ ; not significant) nor calf production per year for females 3 years or older varied between lineages ( $\chi^2 = 0.09$ ;  $n = 161$ ; not significant). But although females of both lineages produced young, all mated only with NL males.

The extent to which lineage affected male reproduction was further examined by matching 37 (32 NL and all 5 CL) males by age to compare the number of offspring sired over a 4-year period; between-year contrasts were avoided because different numbers of females were available in each year and age must be controlled (Clutton-Brock et al. 1982). Of 131 matings that resulted in offspring, only 19 of the 37 males bred. All were from the NL lineage and none from the CL (Fig. 1a). To determine if this lack of reproduction resulted from a sampling bias due to a low number of CL males or as a biological consequence of poor CL competitive ability, we examined three possibilities. First, we used a binomial coefficient to determine that the probability that all five CL males would be selected at random from the total sample of nonbreeding males was 0.011. Therefore, the lack of reproduction by CL males would not have been predicted solely by their frequency in the population. The difference in lack of breeding by CL males was not an artifact of less intensive sampling because, on average, CL males were actually observed 50% more than NL males (hours per CL male = 67.6 versus 45.9 for NL male;  $t = 2.15$ ;  $n = 5, 32$ ;  $p < 0.05$ ). Second, we compared the percentage of time (hours) that males of each lineage spent in defense of females (time in consort/total time spent in groups during the rut). NL males spent nearly 280% more time in female defense (NL mean [ $\pm$  SE] =  $18.5 \pm 2.4\%$ , CL =  $6.6 \pm 2.0\%$ ;  $Z = 2.44$ ;  $p < 0.01$ ). In fact, CL males were nearly 1.8 times more likely than NL males to cease such defense when approached by competitors (58% versus 33%, respectively;  $\chi^2 = 18.47$ ;  $n = 364$ ;  $p < 0.001$ ). Such data may be criticized because individuals of one lineage or the other may consistently attract larger (or smaller) opponents. Therefore we considered interactions between CL and NL males of the same age when body sizes were within one standard deviation; CL males were displaced nearly 2.7 times more often ( $\chi^2 = 5.54$ ;  $n = 26$ ;  $p < 0.02$ ), a strong indication of low social standing. These results indicate that (1) CL males were more timid, less aggressive, less able to defend females, and less competitive than NL males and (2) not only is the probability of CL males breeding low, but this lineage is becoming extinct (CL-specific alleles on the Y chromosome are presumed to have already disappeared) as introgression occurs between the NL males and CL females. The latter is especially true if small, slower-growing, hybrid male  $F_1$  offspring of CL females and NL males have poorer reproductive success than large NL males (Fig. 1b).



**Figure 1.** Distribution of offspring, sample sizes (above the bar), and standard error of the mean (bars) in relation to age cohorts of Nebraska (NL) and Colorado (CL) males for the 4-year period 1985–1989 (a). Only single CL males exist in each cohort, none reproduced. Individuals in each category are 4 years older at end of study; for example, the results show reproductive contributions for the CL male and NL males (in age 4 cohort) through the ages of 4–7 years inclusive. Comparison of bison calf growth rates of  $F_1$  NL  $\times$  NL (squares = inbred) and NL  $\times$  CL (triangles = outbred) matings (b). Regression lines are significant ( $p < 0.001$ ), explain 75% and 66% of the variance in body mass, respectively, and differ from one another ( $t = 3.88$ ;  $df = 63$ ;  $p < 0.001$ ). Adapted from Berger and Cunningham (1994).

### Social Group Extinction among Coatis

Because the coati bands on Barro Colorado were habituated and recognizable to human observers, year-to-year fluctuations in the size of bands could be followed (Fig. 2). Between 1987 and 1993 the population size was relatively stable; from 1989 to 1993 none of the study bands became extinct. In fact, two bands formed via fission events, and laboratory genetic analyses show that one of these events involved division along lines of relatedness (Gompper et al. 1997). An El Niño event in 1992 caused poor fruiting of many important tree species during 1993 and 1994, resulting in concurrent poor reproduction

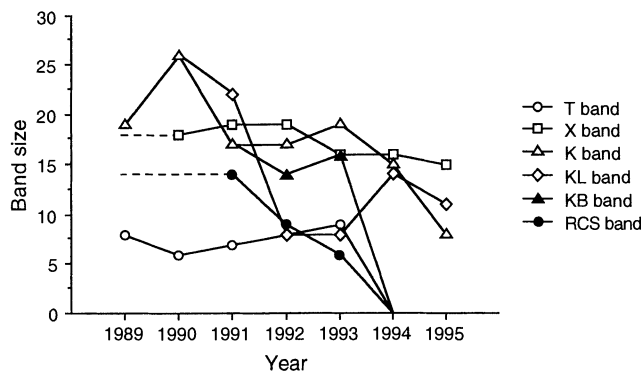


Figure 2. Size of white-nosed coati bands studied on Barro Colorado Island between mid-1989 and late 1995. Three of the smallest bands went extinct in 1994 (based on January 1995 census data). Dashed lines indicate that a band was present but the size of the band was unknown. One additional band was known to be present throughout the study, although the size of the band was never ascertained. Band K split in 1990 and again in 1991.

and possibly higher mortality in 1994. When the population was recensused in early 1995, three of seven study bands had gone extinct, including two of five bands present in 1989 when the study began (Fig. 2). The three failed bands represented the smaller of the six closely monitored bands, which suggests that extinction of coati bands may depend on group size. Surviving bands contained few juveniles (recognizable by body size), indicating a poor breeding season in 1994. Numbers of solitary adult males also declined, indicating increased mortality during 1994 (Gompper, unpublished data). Thus, relatively common catastrophes can lead to the sudden loss of lineages in previously stable populations.

The extinction of social groups due to catastrophic phenomena has been documented in a broad array of mammals. But we lack understanding about which groups within a population are at greater risk of extinction. The observation that only the small coati bands went extinct, likely due to simultaneous effects of emigration by maturing males, mortality of older females, and no cohort of maturing females to replace these older females, would not have been predictable (or understandable a posteriori) without a detailed knowledge of coati natural history. Social groups of other species are likely to react to catastrophes in ways which are, a priori, similarly unpredictable. For example, contact among individuals in social groups may lead to increased transmission of pathogens within social groups. This may in turn lead to the rapid demise of entire groups, while neighboring groups remain unaffected (Chapman 1978; Mills 1990). Pathogens may differ in virulence and persistence in host social groups of different sizes, perhaps leading to differen-

tial extinction rates of large and small groups. Given that catastrophes such as famine or disease are not necessarily rare or unpredictable, there is a great need for further work on these events and their influence on lineage persistence.

### Lineage Loss in Other Mammal Species

Based on the limited data available from other long-term studies of mammals in the literature, we were also able to estimate the loss of matrilineages for 15 species in six orders (Table 1): ungulates, primates, carnivores, pinnipeds, rodents, and hyracoidea (for wild dogs we also examined patriline loss because males are the philopatric sex; Frame et al. 1979). There was a significant relationship between  $\log(\text{female weight})$  and  $\text{logit}(\% \text{ lineages retained})$  ( $r^2 = 0.66$ ;  $p < 0.0001$ ). Small-bodied species such as viscachas, marmots, ground squirrels, or hyraxes retained from 13% to 46% of the lineages over 3–22 years, but species the size of lions, black bears, yellow baboons, red deer, or elephant seals retained from 63% to 97% of the matrilineages over 20-year periods. The relationship between female weight and percentage of lineages retained per year of study was nonsignificant (Table 2), however, suggesting that the apparent importance of body size is an artifact of the length of the various studies or of the generation time of the study species.

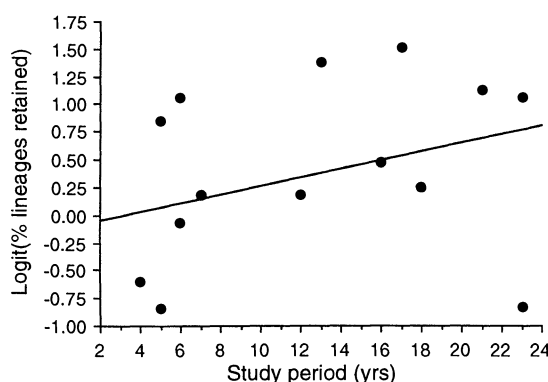
If the loss of lineages is a random process caused by environmental and demographic stochasticity, we would expect a decreasing relationship between the length of the study and the portion of lineages retained in the population. But this was not observed (Table 2; Fig. 3). In fact, when a single outlier—the marmot—is excluded, the opposite pattern is observed: the logistic regression is positive and significant ( $r = 0.61$ ;  $p = 0.018$ ). The age of first reproduction is inversely related to the percentage of lineages retained, however, and it explained 34% of the variance (Fig. 4a), suggesting that species with shorter generation times experience faster turnover in lineages. But when age of first reproduction is regressed against the percentage of lineages retained per year of study, the relationship is not significant (Table 2; Fig. 4b). Because small species may have shorter generation times than large species, they may be studied over more generations than large species. Thus the duration of the individual studies should be incorporated into the analysis. We did this by dividing the number of years a species was studied by its age of first reproduction. There was no significant relationship between this parameter and the percentage of lineages retained (Table 2; Fig. 5). In other words, both body size and generation time are poor predictors of the rate at which lineages are lost across species.

Although our data included six orders and 15 species, the possibility also exists that phylogenetic history influ-

**Table 2.** Regression analyses of lineage retention across mammal species, families, and orders.

Analysis	Regression equation	r	p
Species level ( $n = 14$ )			
length of study versus logit(% lineages retained)	$y = -0.12 + 0.038x$	0.34	0.218
log(female weight) versus logit(% lineages retained/year)	$y = -1.351 + 0.086x$	0.26	0.367
log(age of first reproduction) versus logit(% lineages retained)	$y = -0.272 + 1.716x$	0.58	0.021
log(age of first reproduction) versus logit(% lineages retained/year)	$y = -1.268 + 0.009x$	0.01	0.980
log(length of study/age of first reproduction) versus logit(% lineages retained)	$y = 0.874 - 0.836x$	-0.20	0.483
Family level ( $n = 11$ )			
length of study versus logit(% lineages retained)	$y = -0.137 + 0.053x$	0.43	0.165
log(female weight) versus logit(% lineages retained/year)	$y = -1.384 + 0.119x$	0.30	0.346
log(age of first reproduction) versus logit(% lineages retained)	$y = -0.142 + 1.704x$	0.56	0.059
log(age of first reproduction) versus logit(% lineages retained/year)	$y = -1.274 + 0.129x$	0.10	0.771
log(length of study/age of first reproduction) versus logit(% lineages retained)	$y = 1.038 - 0.83x$	-0.21	0.522
Order level ( $n = 6$ )			
length of study versus logit(% lineages retained)	$y = -0.225 + 0.59x$	0.37	0.502
log(female weight) versus logit(% lineages retained/year)	$y = -1.551 + 0.239x$	0.65	0.184
log(age of first reproduction) versus logit(% lineages retained)	$y = 0.018 + 1.15x$	0.31	0.582
log(age of first reproduction) versus logit(% lineages retained/year)	$y = -1.463 + 0.598x$	0.37	0.502
log(length of study/age of first reproduction) versus logit(% lineages retained)	$y = 0.492 - 0.059x$	-0.02	0.975

ences the relationship. We therefore repeated the analysis at the family level ( $n = 12$ ), including the means of the three sciurid rodents (2 species of ground squirrels and the marmot) and two cercopithecoid primates (yellow baboons and toque macaques), and at the order level ( $n = 6$ ) using the means of family values (two rodent families and six carnivore families). All regression analyses were consistent with the prior analysis that included all species (Table 2), with the exception that the relationship between lineage retention and age of first reproduction was weaker (at the family level;  $r^2 = 0.31$ ;  $p = 0.06$ ) or nonexistent (at the order level;  $p = 0.58$ ). Unfortunately, without additional data on lineage loss in more species of mammals living under unmanaged conditions, it will remain difficult to untangle the relative effects of body size and phylogeny on the rate with which lineages are lost in a population.



**Figure 3.** Logistic regression between length of the study and the percentage of lineages retained at the end of the study ( $p = 0.218$ ).

#### Variable Reproductive Success in Acorn Woodpeckers and Other Birds

Acorn Woodpeckers are cooperative breeders, and most juveniles either spend their entire lives on their natal territory or move only a short distance before breeding. This limited dispersal makes it possible to examine both variance in lifetime reproductive success and persistence of specific family lineages. In the population in central New Mexico studied between 1975 and 1984, 69% of males and 74% of females that established breeding territories failed to produce even one future breeder in the population (Fig. 6). Of the family groups occupying 20 territories, seven went extinct without producing any young that subsequently bred, while five (20%) produced 59% of all future reproductive individuals. Whether or not a group bred successfully was highly dependent upon the quality of the territory possessed by that group (Stacey & Ligon 1987, 1991).

A similar pattern also has been observed in the cooperatively breeding Green Woodhoopoe (*Phoeniculus purpureus*; Ligon & Ligon 1988; Stacey & Ligon 1991; D. Ligon, personal communication). Only 5 of the 16 family groups studied between 1975 and 1982 and during 1984 produced new breeders, and the remaining 11 served as sinks for nonbreeders. Lineage turnover (extinction followed by territorial recolonization by unrelated individuals from productive lineages) occurred at least once on each of these territories (Ligon & Ligon 1988).

Current evidence indicates that lineage loss is common among birds, although detection of turnover rates is complicated by the fact that, unlike among mammals, both males and females normally disperse before reproducing (Greenwood 1980), and these birds are often lost from the sample of individuals under observation. Long-



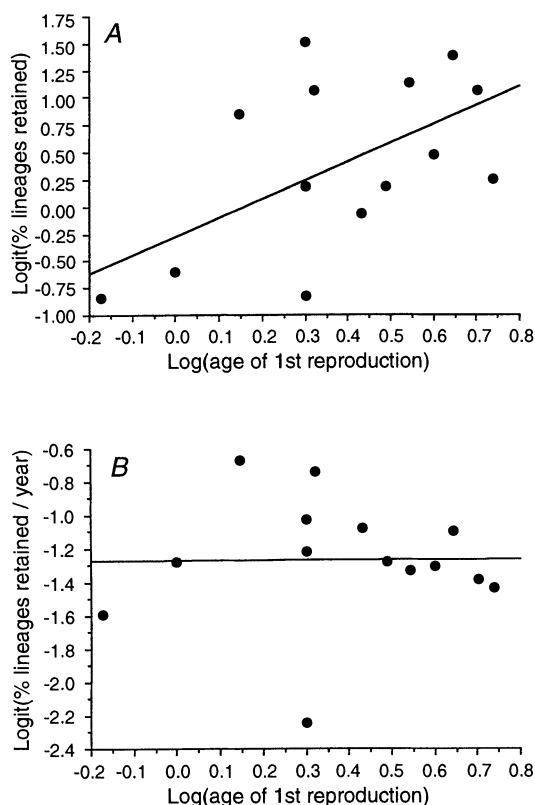


Figure 4. Logistic regression between the age of first reproduction and the percentage of lineages retained at the end of the study ( $p = 0.021$ ) (a). Logistic regression between the age of first reproduction and the percentage of lineages retained per year of the study ( $p = 0.980$ ) (b).

term studies have shown that, for a wide variety of species, variation in lifetime reproductive success is extremely high, and most individuals never produce surviving offspring (Clutton-Brock 1988; Newton 1989; Stacey & Koenig 1990). The asymmetry in reproductive success is even more extreme when the number of offspring that themselves become breeders is examined: in 23 small and large-bodied species discussed by Newton (1989), 40–70% of even those birds that survived long enough to begin breeding did not contribute offspring who successfully bred to the next generation. Thus, the effective breeding population is typically much smaller than the actual number of potential breeders, and many genetic lineages will be lost simply by chance (Crow & Kimura 1970).

## Conclusions and Challenges

Our findings reaffirm the observation that even in fairly large populations many potential breeders never leave surviving offspring, and as a result many potential ge-

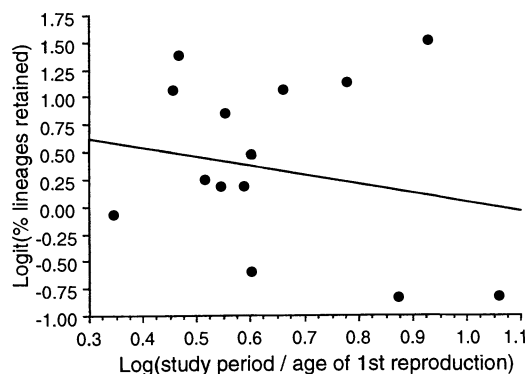


Figure 5. Relationship between percentage of lineages retained and the maximum number of generations that could have occurred during the study, calculated as the length of the study divided by the age of first reproduction ( $p = 0.483$ ).

netic lineages are lost. Irrespective of the mechanisms affecting population structure, which may range from stochastic environmental and genetic events to behavioral phenomena like the poor intrasexual competitive abilities of one line of bison at Badlands NP, lineages can be lost quickly from natural (or restored) populations. In the few cases where it has been systematically examined, particularly in birds, production of future breeders is nonrandom and is generally confined to a few families, at least over relatively short periods of a decade or so. It is likely that the same pattern exists in mammals. Even in captive or reintroduced populations, lineages are regularly lost (Geyer et al. 1989; Stanley-Price 1989; Berger & Cunningham 1994) despite the effort of management to retain underrepresented lines. Therefore, the extent to which the artificial retention of alleles by the management of breeding structures or individual reproductive success can actually lessen inbreeding depression or allow further adaptive evolutionary responses to changing environments is uncertain.



Figure 6. The number of future breeders produced by male and female Acorn Woodpeckers in Water Canyon, New Mexico, 1975–1984.

One of the more interesting results of these analyses is that, after correcting for the length of the study period and assuming minimum generation time, the rate of lineage loss per generation was not dramatically different among the mammal species for which we had data. The smaller species (rodents and the hyrax) lost 8–24% of lineages per generation, whereas the larger species (carnivores, primates, and ungulates) lost 0.4–11% of lineages per generation. Similarly, in birds, less than half of individuals that are born do not contribute breeding offspring to the next generation in most of the species for which data is available, although the fact that these losses are concentrated in specific lineages can be determined for only two species, Acorn Woodpeckers and Green Woodhoopoes. Lineage loss necessarily decreases the genetic effective size of the population ( $N_e$ ) through time. Lande (1995) has shown that for quantitative characters to maintain adaptive potential in the face of environmental and demographic stochasticity,  $N_e$  should be about 5000. Unlike some processes that effect  $N_e$  (Crow & Kimura 1970; Harris & Allendorf 1989; Hartl & Clark 1989), however, lineage loss may not be a random process but can result from specific ecological or behavioral processes such as mating ability in bison, group size in coatis, and possession of high-quality territories in Acorn Woodpeckers. To the extent that these processes result in directional selection in free-living populations, the  $N_e$  needed to maintain adaptive potential will be even greater than that estimated by Lande (1995). The practicality of attaining these  $N_e$  sizes are interesting problems for which few data on vertebrates are yet available.

These results point to future analytical challenges. First, although they substantiate that body size, habitat quality, variance in reproductive success, differential mortality, and interpopulation movements vary in their effects on lineage loss, data are insufficient to determine the relative contribution of each factor in different species. Clarification must await data on lineage extinction from a far greater number of field studies. Second, long-term genetic losses must be ascertained even though habitat fragmentation will continue to decrease population sizes and make the detection of lineage losses in nonperturbed populations more difficult. Third, our data revealed the reproductive success only of individuals that were resident within the population, and we were not able to examine the long-term consequences of immigration on genetic structure. Such dispersing individuals, if founders of successful lineages in their new populations, may create a local genetic “metapopulation” and help “rescue” small populations from an eventual deterioration of genetic diversity (Maruyama & Kimura 1980; Gilpin 1991; Stacey & Taper 1992; Hastings & Harrison 1994; Backus et al. 1995; Stacey et al. 1996). But given the frequent loss of lineages among even the established breeders as indicated by these results, it is unclear whether or not most immigrants will actually have an impact on

the genetic population structure. And, as the habitats of most species become increasingly fragmented and immigration between populations more difficult, such genetic rescue may become even less common.

These results also raise a philosophical issue that requires broad discussion. Although our findings can be used to justify the idea that the loss of lineages is acceptable because it represents “normal” processes, caution must be exercised because human activity undoubtedly will exacerbate such losses. While lineage losses may be regular events in wild populations and may even occur in managed reserves despite attempts to prevent them, it will take creative tactics to determine how best to apply data on natural losses in the wild to managed populations. Artificial retention of some lineages may simply be a prolongation of genes that would otherwise be selected against in small or reintroduced populations. But alleles that may be disadvantageous in captive populations may be advantageous in the wild. Therefore, without knowing whether lineage loss is a random or a selectional process, it may be prudent to maintain maximal genetic diversity in captive populations, particularly those founded by a small number of individuals already depauperate in genetic diversity. In the long term, it will be important for conservation strategists to decide not only which lineages should be retained but how best to predict which ones will be lost.

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