

Inbreeding Depression in the Speke's Gazelle Captive Breeding Program

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Abstract: *The Speke's gazelle (Gazella spekei) captive breeding program has been presented as one of the few examples of selection reducing the genetic load of a population and as a potential model for the captive breeding of endangered species founded from a small number of individuals. In this breeding program, three generations of mate selection apparently increased the viability of inbred individuals. We reanalyzed the Speke's gazelle studbook and examined potential causes for the reduction of inbreeding depression. Our analysis indicates that the decrease in inbreeding depression is not consistent with any model of genetic improvement in the herd. Instead, we found that the effect of inbreeding decreased from severe to moderate during the first generation of inbreeding, and that this change is responsible for almost all of the decline in inbreeding depression observed during the breeding program. This eliminates selection as a potential explanation for the decrease in inbreeding depression and suggests that inbreeding depression may be more sensitive to environmental influences than is usually thought.*

Depresión por Intracruza en el Programa de Reproducción en Cautiverio para la Gacela de Speke

Resumen: *El programa de reproducción en cautiverio para la gacela de Speke (Gazella spekei) ha sido presentado como uno de los pocos ejemplos de selección que reducen la carga genética de una población y un modelo potencial para la reproducción en cautiverio de especies en peligro fundado a partir de un número pequeño de individuos. En este programa de reproducción, tres generaciones de selección de pareja incrementaron aparentemente la viabilidad de individuos con intracruza. Realizamos el registro genealógico de las gacelas de Speke y examinamos las causas potenciales de reducción de depresión por intracruza. Nuestro análisis indica que la disminución en la depresión no es consistente con ningún modelo de mejoramiento genético en el grupo. Sin embargo, encontramos que el efecto de intracruza disminuyó de severo a moderado durante la primera generación de intracruza, y que este cambio es responsable de casi todas las disminuciones de la depresión por intracruza observadas durante el programa de reproducción. Esto elimina a la selección como una explicación potencial de la disminución de la depresión, y sugiere que la depresión por intracruza puede ser más sensible a influencias ambientales de lo que actualmente se cree.*

Introduction

Starting in the late 1970s, inbreeding was documented to cause a substantial reduction of fitness in captive populations of endangered species (e.g., Ralls et al. 1979;

Ralls et al. 1988). For example, Ralls et al. (1988) estimated that full-sib mating increased juvenile mortality by 33%, on average, compared to noninbred births. This and subsequent research has shown that inbreeding affects many traits, although to different degrees in different species, populations, and lineages (e.g., Ralls et al. 1988; Pray & Goodnight 1995; Kärkkäinen et al. 1996; Lacy et al. 1996). Avoidance of inbreeding has become a primary goal in the management of small populations.

Inbreeding is unavoidable, however, in populations founded from a small number of individuals. This prob-

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lem has motivated interest in eliminating the genetic basis of inbreeding depression through carefully controlled breeding and selection. Typically, a purging process is envisioned: recessive alleles are exposed to selection by inbreeding, and healthy animals are used for subsequent matings. The success of purging is expected to depend strongly on characteristics of the loci causing inbreeding depression. For example, inbreeding depression caused by increased homozygosity of deleterious recessive alleles can, in theory, be purged, especially when such alleles are few in number and have a large effect. In contrast, inbreeding depression caused by increased homozygosity at loci with heterozygote advantage cannot be purged.

Soon after inbreeding was recognized as potentially harmful to captive populations, Templeton and Read (1983) described a breeding program that appeared to eliminate inbreeding depression from the captive population of the endangered Speke's gazelle (*Gazella spekei*). Templeton and Read selected mating pairs for approximately 3 years and claimed that this pedigree management substantially increased the viability of inbred gazelles. They attributed this accomplishment to selection against deleterious alleles and selection for favorable allele combinations made possible by inbreeding and recombination (e.g., Templeton & Read 1994).

This breeding program received much attention in the conservation biology community and has been followed by extensive investigation of the relationships among genetic variation, fitness, selection, and population size. Inbreeding depression is present in many species, but its genetic basis and response to selection has proven complex. Experimental attempts to reduce the effect of inbreeding in small populations of outcrossing organisms have not replicated the dramatic results of the Speke's gazelle captive breeding program. Also, the potential for deliberate inbreeding to increase the probability of population extinction has been emphasized (Hedrick 1994). Modern captive breeding programs now seek to maximize the retention of genetic variation (Ballou & Foose 1996) using breeding strategies that are still being refined (S.T.K., unpublished data). The less conventional claims of Templeton and Read (1984) that recombination decreased inbreeding depression have received less attention.

Although the breeding methods of Templeton and Read have not been adopted by modern population managers, the Speke's gazelle breeding program has become an important case study in the conservation biology literature and is often cited in conservation-oriented discussions of inbreeding depression (e.g., Pennisi 1999). Several authors have questioned both the plausibility of Templeton and Read's explanations and the validity of their analysis. Templeton and Read (1998) have successfully responded to critics of their statistical methods (Lacy 1997a; Willis & Wiese 1997), but other issues have not been explicitly examined. For example, He-

drick (1994) doubted that the limited amount of inbreeding in the pedigree could have reduced inbreeding depression to the extent observed, and Frankham (1995) suggested that the decline in inbreeding depression might have been caused by the establishment of a second population in a zoo with a more favorable climate.

These issues remained unresolved because alternative explanations for the observations of Templeton and Read have not been analyzed in detail and because the plausibility of the chosen hypothesis has not been thoroughly evaluated. We used a combination of data analysis and visualization to show that previous analysis of the Speke's gazelle breeding program failed to reveal an important characteristic of the data. We argue that this lapse, along with the lack of alternative explanations, led to inappropriate biological conclusions.

Speke's Gazelle in Captivity: 1970–1982

From 1970 to 1982, the captive population of Speke's gazelles in the United States was descended from four wild-born individuals that were transferred to the St. Louis Zoo by 1972: one male (studbook number 6) and three females (nos. 7, 8, 9). No additional founders were added to the herd until 1992. By 1979 the herd had increased from the initial four founders to 19 animals (Templeton & Read 1983).

The breeding program of Templeton and Read began in February 1980, although some of the previous matings were also planned by Templeton and Read (A. Templeton, personal communication). Two criteria were used to select individuals to breed (Templeton & Read 1983): (1) breeders were chosen to help equalize founder representation in the herd, and (2) healthy inbred animals were used preferentially as parents. Two criteria were used to determine mating pairs among the individuals selected to breed (Templeton & Read 1983). Mating pairs were chosen to produce offspring that descended from as many founders as possible and were inbred but not to excess. Because this breeding program differed from the modern goal of retaining maximum genetic diversity in a population, it probably retained less genetic variation than might have been possible. The difference, however, between the breeding program of Templeton and Read and that of maximum retention of genetic variation or maximum avoidance of inbreeding was probably small.

Modeling the Effect of Inbreeding on Viability

The relationship between inbreeding and viability is usually modeled as

$$S = S_0 e^{-Bf} \quad (1)$$

Table 1. Number of births and survivors to 30 days in each inbreeding class, f , for captive Speke's gazelles born to noninbred and inbred parents.

f	Offspring of noninbred parents		Offspring of inbred parents	
	born	survived	born	survived
0.0000	26	20	—	—
0.0625	1	1	1	1
0.0938	—	—	1	1
0.1094	—	—	3	2
0.1250	10	7	17	12
0.1563	—	—	3	2
0.1875	1	1	5	3
0.2031	—	—	1	1
0.2500	23	8	6	3
0.2813	—	—	3	3
0.3125	—	—	2	1
0.3438	—	—	3	2
0.3750	—	—	3	2
Total	61	37	48	33

(Morton et al. 1956), where S is the probability of an individual with the inbreeding coefficient f surviving to a specified age, S_0 is the viability of noninbred individuals, and B is a measure of how fast viability declines with inbreeding. Also, B is approximately equal to the number of lethal equivalents present in a doubled haploid genome. A lethal equivalent is a unit of genetic variation that measures the potential effect of deleterious alleles on viability. For example, an allele or set of alleles that causes death 50% of the time constitutes 0.50 of a lethal equivalent. This model assumes that loci affecting viability are multiplicative and independent in action and that viability is unaffected by variables such as year and location of birth.

Methods and Results

We sought to reconstruct the data and replicate the analytic methods of Templeton and Read, as appropriate. Templeton and Read examined the effect of inbreeding on two Speke's gazelle data sets: (1) all births through July 1982 (Templeton & Read 1983) and (2) all births through 1983 (Templeton & Read 1984). We reanalyzed the original data set. We obtained the birth date, birthplace, death date, and parents of each gazelle from the Speke's gazelle studbook (Fisher 1993). Following Templeton and Read, we defined viability as survival to 30 days. We calculated inbreeding coefficients for all births (Ballou 1983) and followed Templeton and Read's (1983, 1984) division of the pedigree into two categories: births with noninbred parents and births with at least one inbred parent. We defined $B_{\text{noninbred}}$ as the number of lethal equivalents in the offspring of noninbred parents and B_{inbred} as

the number of lethal equivalents in the offspring of inbred parents.

By the end of July 1982, 109 gazelles had been born in captivity and the third generation of inbreeding had begun (Table 1). Of the 109 offspring, 61 had noninbred parents and 48 had at least one inbred parent. Of the 61 offspring born to noninbred parents, 26 were noninbred and 35 were inbred. All offspring with at least one inbred parent were inbred.

We were unable to reconstruct exactly the data of Templeton and Read (1983). The studbook data set has a different number of individuals than that of Templeton and Read (1983) (Table 2). This is probably because their data contained a few minor errors (Templeton & Read 1984). Because our data set is slightly different than that of Templeton and Read (1983), and because we used a recently developed method to estimate B which is less biased (Kalinowski & Hedrick 1998), we repeated some of their analysis.

Inbreeding Depression in the Speke's Gazelle Pedigree

Using the data in Table 1, we obtained 2.60 as a maximum likelihood (Kalinowski & Hedrick 1998) estimate of $B_{\text{noninbred}}$, with a 95% confidence interval of [0.81, 4.79] (Figs. 1a & 2a). For births with inbred parents we obtained 0.57 as an estimate of B_{inbred} , with a 95% confidence interval of [0, 2.89]. Estimates of $S_{0,\text{inbred}}$ and $S_{0,\text{noninbred}}$ were 0.79 and 0.77, respectively. Both estimates of S_0 were similar to the observed viability of noninbred births, 0.77. If we assume that S_0 was equal for both sets of births, we obtain $\hat{S}_0 = 0.79$, $\hat{B}_{\text{noninbred}} = 2.59$, $\hat{B}_{\text{inbred}} = 0.69$ (where \hat{S}_0 indicates an estimate of the actual value of S_0 , etc., and \hat{B} indicates an estimate of the actual value of B). These results are similar to those of Templeton and Read (1983) (Table 2). The maximum likelihood confidence intervals show that the estimate of $B_{\text{noninbred}}$ is significantly greater than zero and that the estimate of B_{inbred} is not significantly different from zero.

Table 2. Estimates of S_0 and B for captive-born Speke's gazelles, categorized by inbreeding coefficient of parents and year of birth for this study and an earlier analysis.

Study	n	\hat{S}_0^a	\hat{B}^b
Present			
offspring of noninbred parents	61	0.79	2.60
1970-1975	29	0.74	6.56
1976-1982	32	0.85	1.35
offspring of inbred parents	48	0.77	0.57
Templeton and Read (1983)			
offspring of noninbred parents	64	0.80	3.09
offspring of inbred parents	46	0.81	1.35

^a \hat{S}_0 , viability of noninbred individuals.

^b \hat{B} , speed with which viability declines with inbreeding.

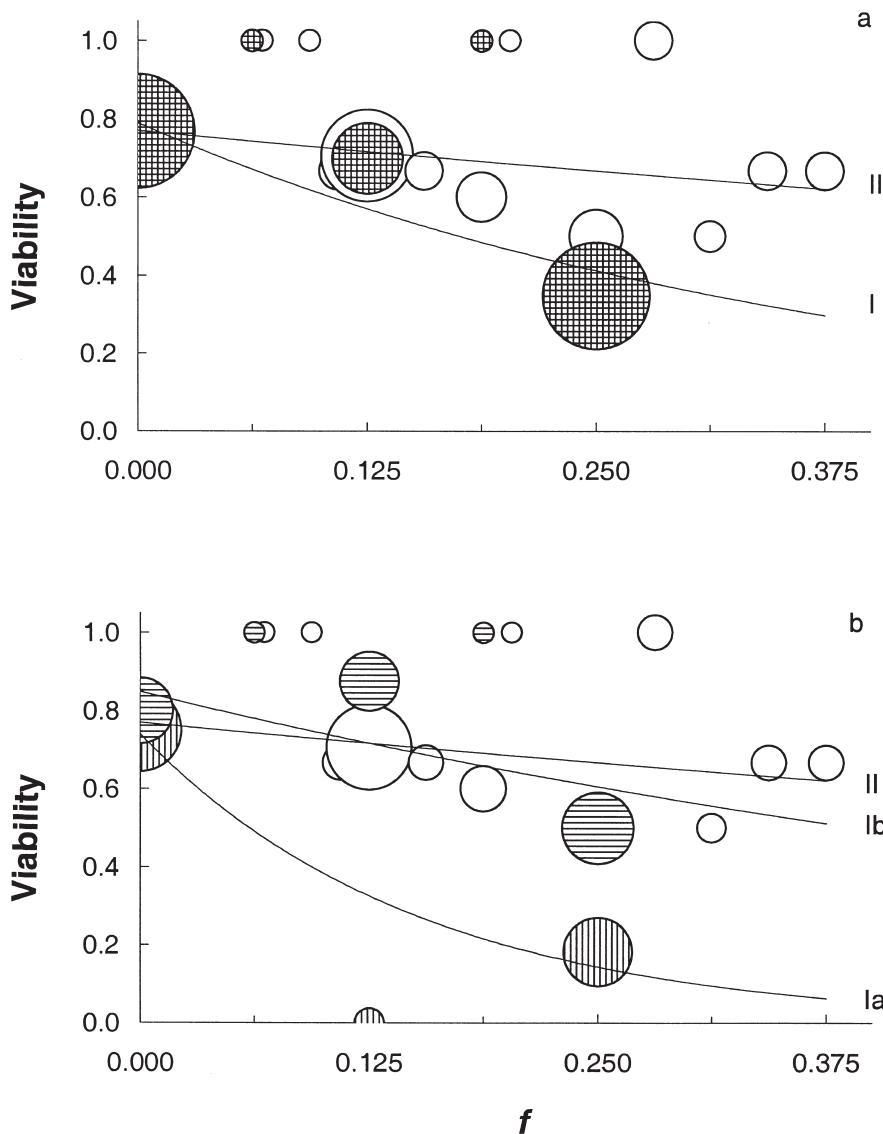


Figure 1. Observed viability (circles) and fitted viability (curves, using the model of Morton et al. 1956) as a function of inbreeding coefficient for gazelles categorized by (a) parental inbreeding coefficient and (b) both year of birth and parental inbreeding coefficient: all offspring of noninbred gazelles (cross hatched circles, curve I), offspring of noninbred gazelles born prior to 1976 (vertically lined circles, curve Ia), offspring of noninbred gazelles born in 1976 or later (horizontally lined circles, curve Ib), and offspring of inbred gazelles (open circles, curve II).

We now ask if the apparent reduction in inbreeding depression, from $\hat{B}_{\text{noninbred}} = 2.60$ to $\hat{B}_{\text{inbred}} = 0.57$, could have been caused by chance alone. To address this question, we used a randomization test similar to that recommended by Templeton and Read (1998). In this test and in others described below, our null hypothesis was that each set of gazelles belongs to the same population. Our alternative hypothesis was that each set of gazelles came from a population with a different number of lethal equivalents but the same noninbred viability (Fig. 2a). For each randomization of the data, we estimated $\hat{B}_{\text{noninbred}}$ and \hat{B}_{inbred} (assuming that $S_{0,\text{inbred}}$ and $S_{0,\text{noninbred}}$ were equal) and calculated the test static, T :

$$T = \hat{B}_{\text{noninbred}} - \hat{B}_{\text{inbred}}. \quad (2)$$

After 50,000 randomizations of the data, we obtained an achieved level of significance of 0.019, which is similar

to the estimate of 0.0015 obtained by Templeton and Read (1998).

Role of Selection upon Inbreeding Depression

Several hypotheses can explain the observed reduction in inbreeding depression. We first addressed the view of Hedrick (1994) that two to three generations of inbreeding are not sufficient to reduce the effect of inbreeding upon viability to the extent observed. We used simulated gene transmission through the Speke's gazelle pedigree, "gene dropping" (MacCluer et al. 1986), to estimate the proportion of each gazelle's genome that was identical by descent to alleles that had been identical by descent in an ancestor of that gazelle, f_a , and the proportion of each gazelle's genome that was identical by descent to alleles identical by descent for the first time in that gazelle's lineage, f_n . The standard inbreeding coefficient, f , equals $f_a +$

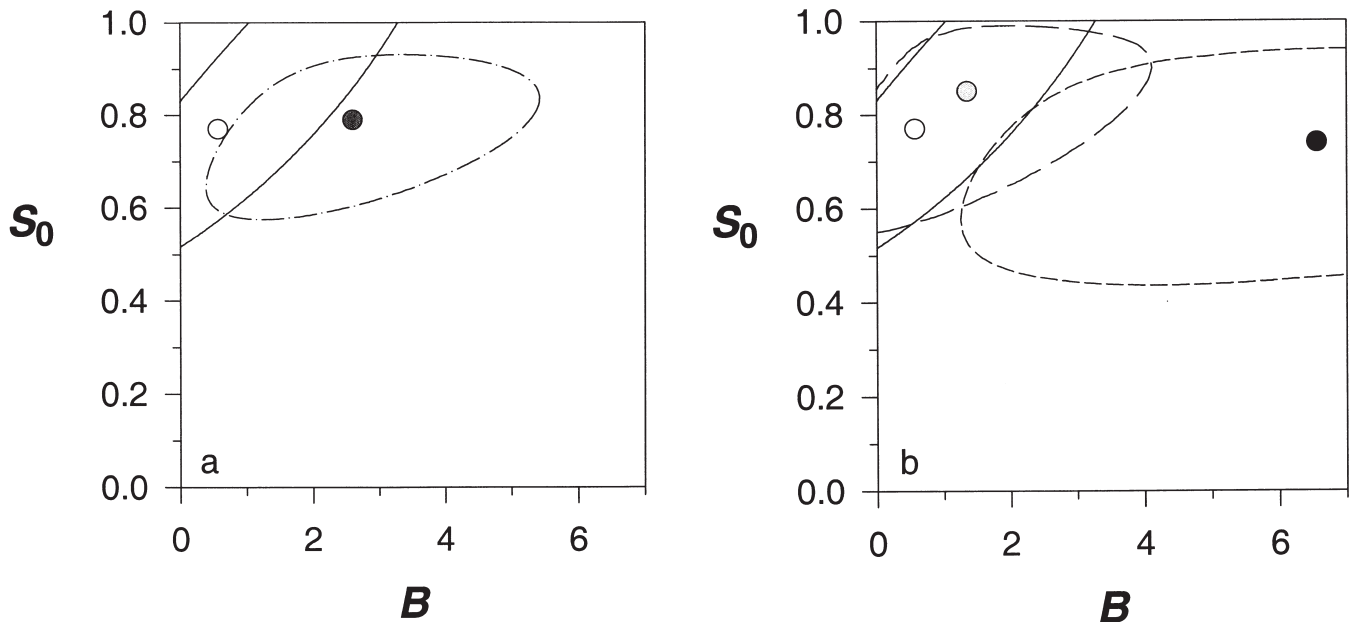


Figure 2. Maximum likelihood estimates of S_0 and B (circles), with 95% confidence regions of these estimates (regions enclosed by curves) for gazelles: (a) contrasts of estimates of S_0 and B for the offspring of noninbred gazelles (darkly shaded circle, dot-dash curve) with the offspring of inbred gazelles (open circle, solid curve); (b) the same data, except that the offspring of noninbred gazelles (darkly shaded circle, dot-dash curve in [a]) have been subdivided into two categories, gazelles born before 1976 (black circle, short dashed curve) and gazelles born in or after 1976 (lightly shaded circle, long dashed curve).

f_n . Our approach differs from that of Ballou (1997), who defines the ancestral inbreeding coefficient as the “cumulative proportion of an individual’s genome that has been exposed to inbreeding in its ancestors.”

Gene dropping revealed two relevant points. First, we found that only 30% of the loci identical by descent in offspring of inbred parents had ancestral inbreeding. Second, we found that the proportion of loci identical by descent for the first time remained roughly constant during the breeding program (Fig. 3). This implies that inbreeding depression should not have declined dramatically (as was observed) during the course of the breeding program.

We quantitatively addressed this unmet expectation with a model of highly efficient purging. Our model of inbreeding depression in a pedigree undergoing selection combines the genetic basis of inbreeding depression used by Morton et al. (1956) with a purging mechanism similar to the lethal recessives model developed by Slatis (1960) and used in a modified form by Ballou (1997). If we assume that inbred individuals who survive have no deleterious alleles at loci identical by descent, then the probability of an individual surviving, S , is

$$S = S_0 \exp(-B_{\text{founders}} f_n), \quad (3)$$

where B_{founders} represents the number of lethal equivalents brought to the breeding program by the founders

of the pedigree. Selection in this model is highly efficient because deleterious alleles are eliminated in the first circumstance that they are identical by descent. This model is different from the traditional method of modeling selection and inbreeding depression because it does not model the decreasing number of lethal equivalents in the pedigree, as we have implicitly done when we compared $\hat{B}_{\text{noninbred}}$ and \hat{B}_{inbred} . The B_{founders} is a constant describing the founders of the pedigree and therefore does not change. We modeled the decreasing probability of individuals dying from genetic causes each generation by estimating the decreasing proportion of genomes that had not been exposed to selection. This model is consistent with both the widely accepted interpretation of the Speke’s gazelle breeding program as an example of purging (e.g., Lynch & Walsh 1998) and mainstream views of how selection and the genetic basis for inbreeding depression interact, but not with the view of Templeton and Read (1984, 1994) that epistasis is important.

Based on the offspring of noninbred gazelles, we estimated B_{founders} to equal 2.60. If our model of purging is accurate, we should obtain a similar estimate of B_{founders} from the offspring of inbred gazelles (our model accounts for the purging effect of selection while doing this). If our model overestimates the efficiency of selection, then we expect the estimate of B_{founders} derived from births with inbred parents to be >2.60 . The oppo-

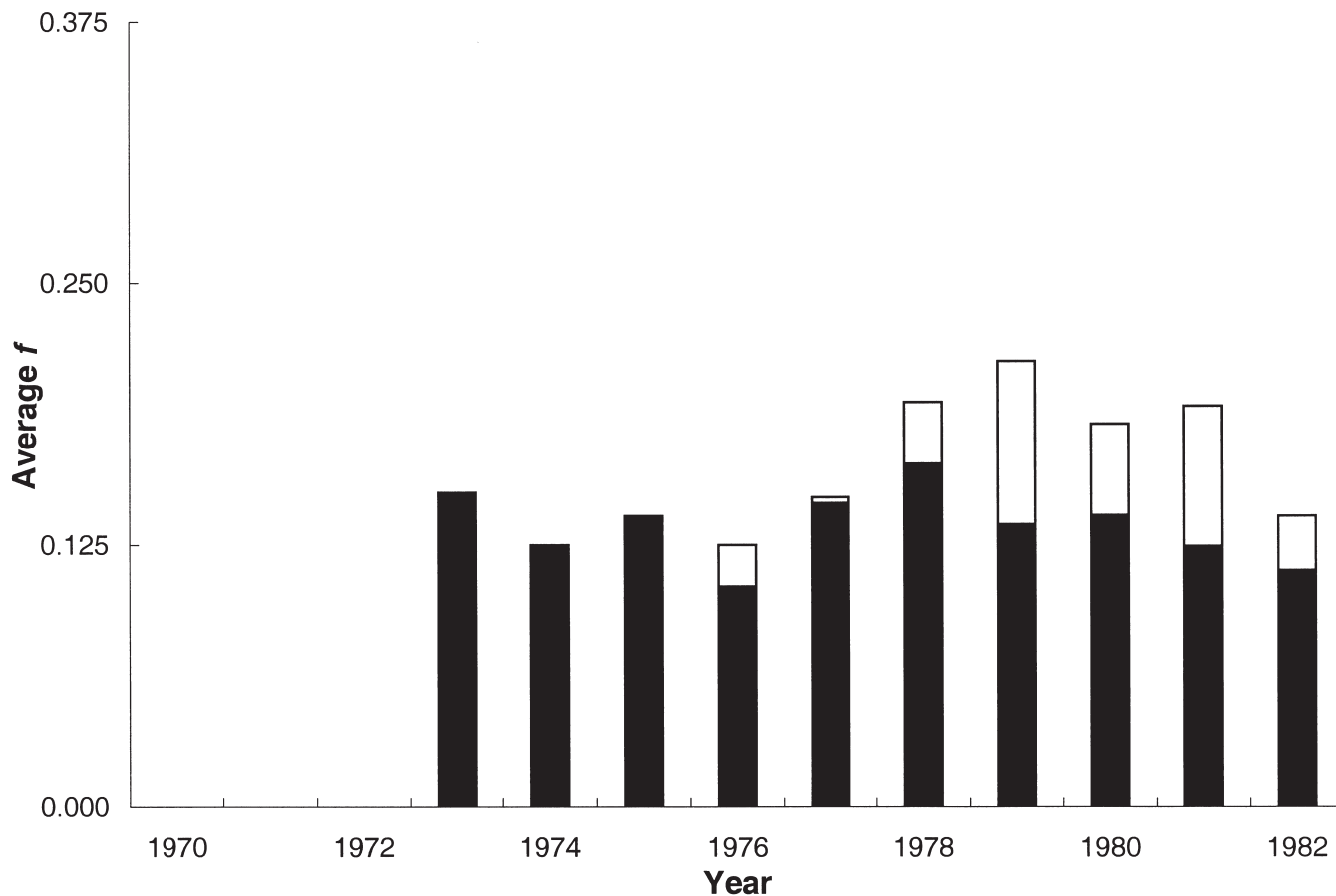


Figure 3. Average proportion of gazelle genomes identical by descent each year partitioned by presence (white) or absence (shaded) of ancestral inbreeding.

site of this occurred, however. Equation 3 estimated B_{founders} to equal 0.09 for the offspring of inbred parents. A randomization test showed that chance alone is unlikely to have caused this difference (achieved level of significance equals 0.04). We concluded that the lethal equivalents present in the founders caused death in the offspring of noninbred parents but not in the offspring of inbred parents.

We rejected our model of selection as inadequate to explain the observed decrease in inbreeding depression. If selection was responsible for the change, it must have operated faster than our maximally efficient single-locus model of purging. Strong epistasis could produce such a result, the explanation favored by Templeton and Read (1994). But before considering this explanation in detail, we would like to rule out less complex possibilities that we believe are more likely.

Potential Effect of Improving Husbandry upon Viability

We have assumed that the rate at which viability declines due to inbreeding is independent of environmental effects, but this may not be appropriate. Examples of

increased heterosis in stressful environments (for review see Barlow 1981) suggests that inbreeding depression might be more pronounced in suboptimal conditions. Therefore, improving zoo husbandry might reduce inbreeding depression without increasing S_0 . Many environmental factors could conceivably exacerbate or ameliorate the effects of inbreeding. For example, Ralls et al. (1988) suggested that the availability of veterinary care, in particular, might reduce inbreeding depression by helping weak, inbred individuals survive that otherwise would not. Recently, evidence for increased inbreeding depression in stressful conditions has accumulated in both controlled environments (e.g., Miller 1994; Pray et al. 1994) and natural environments (e.g., Jimenez et al. 1994; Keller et al. 1994). Inbred gazelles with inbred parents were born later in the breeding program than inbred gazelles with noninbred parents (Fig. 4), so if husbandry conditions improved in a manner that decreased the effect of inbreeding depression, this could explain why $B_{\text{noninbred}}$ appears to be so much larger than B_{inbred} .

In our analysis of this hypothesis, we eliminated potential effects of selection by examining only the first generation of inbreeding. During the breeding program, 61 gazelles were born to noninbred parents. Of these,

roughly half (29) were born prior to 1 January 1976, so we used this date to divide the offspring of noninbred births into two time periods. We found evidence of much stronger inbreeding depression during the first half of the breeding program ($\hat{S}_{0,1970-1975} = 0.74$ and $\hat{B}_{1970-1975} = 6.76$) than during the second half ($\hat{S}_{0,1976-1982} = 0.85$ and $\hat{B}_{1976-1982} = 1.37$) (Figs. 1b & 2b). A conservative randomization test yielded a $p = 0.007$ for this difference. In this test, we did not assume that S_0 remained constant when we estimated each B , although a randomization test using the test statistic $\hat{S}_{0,1976-1982} - \hat{S}_{0,1970-1975}$ showed that the difference in estimates of S_0 was not significant ($p = 0.26$). Therefore, we concluded that viability among inbred gazelles was increasing before the effect of selection could have been evident. This conclusion may appear to contrast with the results of Ballou (1997), who found no evidence for a temporal change in the effect of inbreeding, but Ballou's model assumed that year of birth affected S_0 but not B .

The low viability among inbred gazelles born to noninbred parents from 1970–1975 represents the majority of the inbreeding depression that disappeared during the breeding program (Figs. 1 & 2). In other words, viability

among inbred individuals rose almost exclusively during the first generation of inbreeding. This observation contrasts with the assumption of all previous analyses of this breeding program that inbreeding depression declined after the first generation of inbreeding. (Templeton and Read [1984] discuss reductions during and after the first generation of inbreeding.) Gazelles born during the latter half of the first generation of inbreeding (1976–1982) had approximately the same viability as subsequent generations of inbred offspring (Figs. 1 & 2). Dividing the offspring of inbred gazelles into births with two generations of inbreeding and births with more than two generations of inbreeding revealed the latter half of the breeding program was homogeneous (S.T.K., unpublished data).

Identifying the timing of the reduction in inbreeding depression required us to reframe our investigation. Instead of trying to explain the different viability of first and subsequent generations of inbred births, we attempted to explain the rise in viability during the first generation of inbreeding. Selection is not a viable explanation for this increase, so we did not have to weigh the relative merits of purging and epistatic models. An improvement in hus-

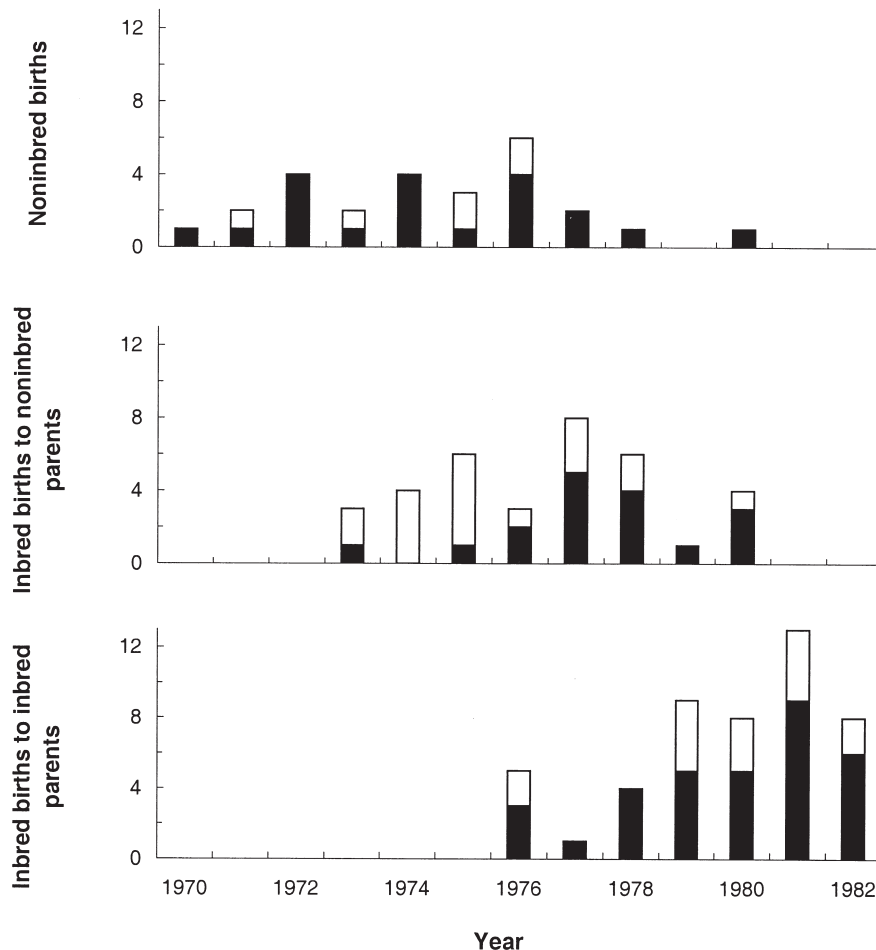


Figure 4. Number of viable (shaded) and nonviable (white) gazelle births each year, categorized by the inbreeding coefficient of parents and offspring.

bandry conditions is our first hypothesis consistent with the data, but we examined other potential explanations, including those favored by Templeton and Read (1984).

Zoo Location and Viability of Inbred Individuals

During the period we analyzed, 89 gazelles were born in St. Louis, Missouri, 19 in Brownsville, Texas, and 1 in San Antonio, Texas. We might reasonably suspect that inbred gazelles had a higher viability in Brownsville than in St. Louis and that this could have produced the observed increase in viability. But only 2 of the 19 gazelles born in Brownsville had noninbred parents, and these 2 were noninbred. Zoo location therefore cannot explain the increased viability of inbred gazelles during the first generation of inbreeding. Furthermore, there did not seem to be less inbreeding depression among the offspring of inbred gazelles in Brownsville than in St. Louis (S.T.K., unpublished data).

Levels of Founder Representation and Magnitude of Inbreeding Depression

Pedigree analysis can assign deleterious traits to particular founders of breeding programs (e.g., Laikre & Ryman 1991), and we attempted to do this for the Speke's gazelle breeding program. If the male founder carried more lethal alleles than the female founders, then Templeton and Read's goal of equalizing founder representation may have increased the viability of inbred offspring. To investigate this possibility, we calculated "partial" inbreeding coefficients, the proportion of an individual's genome that is identical by descent with alleles from a specific founder (Lacy et al. 1996; Lacy 1997b) for each individual. If f_i is the partial inbreeding coefficient for the i th founder, then $\sum_{i=1} f_i$ equals the standard inbreeding coefficient of the individual when summation is taken over all founders. We obtained maximum likelihood estimates of the number of lethal alleles in each of the founders using the model

$$S = S_0 \exp\left(-\sum_{i=1} B_i f_i\right), \quad (4)$$

where B_i is the number of lethal equivalents in the i th founder.

We found that founder 6 was the only one to contribute alleles to loci identical by descent in the offspring of noninbred gazelles from 1970–1975, and therefore that it had an estimated 6.56 lethal equivalents. In addition, founder 6 contributed 65% of the loci identical by descent in the offspring of noninbred parents from 1976–1982 (26% were from founder 7 and 9% from 9). Equation 4 estimated that founder 6 had 0.00 lethal equivalents during the years 1976–1982 (Table 3). The declining contribution of founder 6 to loci identical by descent therefore does not appear to explain the increase in viability that occurred in 1976, although we acknowledge that the data do not permit a strong test of this hypothesis.

Epistasis and Viability during the First Generation of Inbreeding

Templeton and Read (1984) demonstrated that the viability of full- and half-sib matings (hybridity coefficient, $b = 1.0$) was higher than the viability of parent-offspring matings ($b = 0.5$) and concluded that this was because of epistatic interactions associated with recombination of the founder's genomes. This hypothesis neatly explains the rise in viability halfway through the first generation of inbreeding, but hybridity among inbred births is hopelessly confounded with year of birth. All but one of the gazelles born to parent-offspring crosses were born before 1976, and all of the 21 offspring of full- and half-sib crosses were born after 1976.

Templeton and Read (1984, their Tables 6 & 7) also argued that mixed ancestry led to increased viability, but this result can also be explained by a tight association of ancestry coefficients and year of birth. Templeton and Read (1984, their Table 8) showed that mixed ancestry was associated with higher viability among inbred gazelles born between 1976 and 1982. But gazelles born with a limited degree of mixed ancestry (among which viability was low) all had inbreeding coefficients of 0.25, whereas the gazelles born with an increased degree of mixed ancestry (for which viability was high) had an average inbreeding coefficient of 0.125. Therefore, the data are also consistent with simple inbreeding depression.

Table 3. Estimated number of lethal equivalents in each founder of the Speke's gazelle captive breeding program (1970–1982), assuming no purging.*

	S_0	B_6	B_7	B_8	B_9
Offspring of noninbred parents					
1970–1975	0.74	6.56	—	—	—
1976–1982	0.85	0.00	5.19	—	1.94
Offspring of inbred parents	0.88	1.42	1.43	0.00	0.00

* S_0 , estimate of the actual value of S_0 (defined in Table 2), and B_x , estimate of the actual value of B (defined in Table 2).

Discussion

After demonstrating that the apparent decline in inbreeding depression from the first to later generations of inbreeding was not consistent with selection quickly purging deleterious recessives from the Speke's gazelle pedigree, we determined that the most significant event in the breeding program was the increased viability of inbred offspring born to noninbred gazelles. This eliminated selection (with or without epistasis) as a potential explanation. We found no evidence that the increase in viability of inbred individuals was caused by establishment of a breeding program in Brownsville, Texas, or by varying founder representation at loci identical by descent. Two hypotheses were consistent with the increase in viability: improving zoo husbandry and increasing hybridity.

Of these two hypotheses, improving husbandry is more parsimonious and more consistent with other research. The husbandry hypothesis may have the disadvantage of postulating an unknown environmental change, but it does explain the increase in viability of all subsequent inbred births. In contrast, the hybridity hypothesis explains the rise in viability for the first generation of inbred offspring, but not the high viability in the second and third generations (Templeton & Read 1984). Furthermore, outside the *Drosophila* literature (e.g., Charlesworth & Charlesworth 1987; Lynch & Walsh 1998), there is little evidence for the epistasis necessary for the hybridity hypothesis. Although we know of no attempts to look for examples of zoo husbandry ameliorating inbreeding depression, S.T.K. (unpublished data) observed a recent absence of inbreeding depression in a captive species (bighorn sheep [*Ovis canadensis*]) that has shown a strong reduction in viability among captive inbred individuals (Sausman 1984). This change was observed in a population without an opportunity for selection and without an increase in the viability of noninbred births.

Viability among inbred gazelles was low during only the first 3 years of inbreeding, and this occurred early in the breeding program (Fig. 4; only seven noninbred gazelles had been born prior to the first inbred birth). Instead of asking what increased inbred viability from this level, we might more appropriately wonder what caused these handful of deaths. Given the presence of uncontrolled husbandry conditions and multiple potential explanations, a definitive answer seems unlikely.

The Speke's gazelle breeding program has shown that careful management can minimize inbreeding depression. The breeding program, however, does not seem to have eliminated inbreeding depression by the method intended by its designers and therefore is neither a good example of selection reducing inbreeding depression nor a suitable paradigm for the captive breeding of endangered species. Because experimental support for reducing inbreeding depression through controlled inbreeding is weak (e.g., Lacy & Ballou 1998), the current

practice of selecting mating pairs to maximize genetic variation in a population seems most prudent.

Acknowledgments

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Literature Cited

- Ballou, J. D. 1983. Calculating inbreeding coefficients from pedigrees. Pages 509–520 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and conservation*. Benjamin/Cummings, Menlo Park, California.
- Ballou, J. D. 1997. Ancestral inbreeding only minimally affects inbreeding depression in mammalian populations. *Journal of Heredity* **88**:169–178.
- Ballou, J. D., and T. J. Foose. 1996. Demographic and genetic management of captive populations. Pages 263–283 in D. G. Kleiman, S. Lumpkin, M. Allen, H. Harris, and K. Thompson, editors. *Wild mammals in captivity*. University of Chicago Press, Chicago.
- Barlow, R. 1981. Experimental evidence for interaction between heterosis and environment in animals. *Animal Breeding Abstracts* **49**:715–737.
- Charlesworth, D., and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**:237–268.
- Fisher, M. 1993. Speke's gazelle studbook (*Gazelle spekei*). St. Louis Zoological Park, St. Louis, Missouri.
- Frankham, R. 1995. Conservation genetics. *Annual Review of Genetics* **29**:305–327.
- Hedrick, P. W. 1994. Purging inbreeding depression and the probability of extinction: full sib mating. *Heredity* **73**:363–372.
- Jimenez, J. A., K. Hughes, G. Alaks, L. Graham, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* **266**:271–273.
- Kalinowski, S., and P. W. Hedrick. 1998. An improved method for estimating inbreeding depression in pedigrees. *Zoo Biology* **17**:481–497.
- Kärkkäinen, K., V. Koski, and O. Savolainen. 1996. Geographical variation in the inbreeding depression of Scots pine. *Evolution* **50**:111–119.
- Keller, L. F., P. Arcese, J. N. M. Smith, W. M. Hochachka, and S. C. Stearns. 1994. Selection against inbred Song Sparrows during a natural population bottleneck. *Nature* **372**:356–357.
- Lacy, R. C. 1997a. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* **78**:320–335.
- Lacy, R. C. 1997b. Errata. *Evolution* **51**:1025.
- Lacy, R. C., and J. D. Ballou. 1998. Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution* **52**:900–909.
- Lacy, R. C., G. Alaks, and A. Walsh. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. *Evolution* **50**:2187–2200.
- Laikre, L., and N. Ryman. 1991. Inbreeding depression in a captive wolf (*Canis lupus*) population. *Conservation Biology* **5**:33–41.
- Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer Associates, Sunderland, Massachusetts.
- MacCluer, J. W., J. L. Vandeberg, B. Read, and O. Ryder. 1986. Pedigree analysis by computer simulation. *Zoo Biology* **5**:147–160.
- Miller, P. S. 1994. Is inbreeding depression more severe in a stressful environment? *Zoo Biology* **13**:195–208.
- Morton, N. E., J. F. Crow, and J. H. Muller. 1956. An estimate of the mutational damage in man from data on consanguineous marriages. *Proceedings of the National Academy of Sciences of the United States of America* **42**:855–863.
- Pennisi, E. 1999. The perils of genetic purging. *Science* **285**:193.
- Pray, L. A., and C. J. Goodnight. 1995. Genetic variation in inbreeding

- depression in the red flour beetle *Tribolium castaneum*. *Evolution* **49**:176-188.
- Pray, L. A., J. M. Schwartz, G. J. Goodnight, and L. Stevens. 1994. Environmental dependency of inbreeding depression: implications for conservation biology. *Conservation Biology* **8**:562-568.
- Ralls, K., K. Brugger, and J. D. Ballou. 1979. Inbreeding and juvenile mortality in small populations of ungulates. *Science* **206**:1101-1103.
- Ralls, K. J., J. D. Ballou, and A. R. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* **2**:185-193.
- Sausman, K. A. 1984. Survival of captive-born *Ovis canadensis* in North American zoos. *Zoo Biology* **3**:111-121.
- Slatis, H. M. 1960. An analysis of inbreeding in the European bison. *Genetics* **45**:275-287.
- Templeton, A. R., and B. Read. 1983. The elimination of inbreeding depression in a captive herd of Speke's gazelle. Pages 241-261 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and conservation*. Benjamin/Cummings, Menlo Park, California.
- Templeton, A. R., and B. Read. 1984. Factors eliminating inbreeding depression in a captive herd of Speke's gazelle (*Gazella spekei*). *Zoo Biology* **3**:177-199.
- Templeton, A. R., and B. Read. 1994. Inbreeding: one word, several meanings, much confusion. Pages 91-106 in V. Loeschcke, J. Tomiuk, and S. K. Jain, editors. *Conservation genetics*. Birkhäuser-Verlag, Basel, Switzerland.
- Templeton, A. R., and B. Read. 1998. Elimination of inbreeding depression from a captive population of Speke's gazelle: validity of the original statistical analysis and confirmation by permutation testing. *Zoo Biology* **17**:77-98.
- Willis, K., and R. J. Wiese. 1997. Elimination of inbreeding depression from captive populations: Speke's gazelle revisited. *Zoo Biology* **16**:9-16.

