

References and Notes

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6. In our cannulation procedure, an atrial cannula (inner diameter, 0.30 mm; outer diameter, 0.64 mm; 45-cm Silastic tubing, Dow Corning Corp.) exits via a backpack sutured to the mouse and is protected by an extension spring. The entire unit is supported from above and swivels freely. During the 5-day surgical recovery period, 0.33 units of heparin in 0.3 ml of saline is continuously infused per 24 hours. Data to be presented elsewhere (10) document that cannulated males exhibit normal aggressive and sexual behaviors, when compared with males that do not have surgery.
7. The CF-1 mice used in this experiment were reared in our laboratory colony. At weaning (21 to 23 days of age), the males were isolated in 29 by 18 by 13 cm polypropylene cages in a room without females. The ambient conditions were $23^{\circ} \pm 1^{\circ}\text{C}$, 14:10 hour light-dark cycle, lights on at 0600 hours, and Purina mouse chow and water always available. Experimental males were 70 to 80 days old. After cannulation, they were housed in 29 by 14 by 14 cm wooden boxes and remained in the same room. All testing began between 0900 and 1100 hours.
8. After each 25- μl blood sample was obtained, the cannulas were rinsed and the blood was replaced with heparinized saline (10 units per milliliter). The 10- μl samples of plasma were stored in 40- μl radioimmunoassay (RIA) buffer at -80°C before assay. Plasma LH concentrations were determined with the NIAMDD rat radioimmunoassay kit verified for measuring mouse gonadotropins by W. G. Beamer, S. M. Murr, and I. I. Geschwind [*Endocrinology* **90**, 823 (1972)]. The reference curve was fitted and the unknown concentrations were interpolated by using the computer analysis described by D. Rodbard and D. M. Hutt [in *Symposium on Radioimmunoassay and Related Procedures in Medicine* (International Atomic Energy Agency, Vienna, 1974), p. 165]. Within-assay variation was 10.4 percent and between-assay variation 13.9 percent; the minimum detectable amount was 0.125 ng. Results are expressed as nanogram-equivalents of NIAMDD-RAT-LH-RP-1.
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11. Analysis of variance with repeated measures was performed on the peak LH values which were observed during the four sampling periods. Within both patterns of repetitive female exposure, *t*-tests were used to compare the peak LH values observed during the first and fourth sampling periods; the *t*-test between the continuous exposure and repetitive exposure groups compared the peak LH values during the last sampling period.
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14. We are grateful to C. Desjardins for his considerable effort and direction during development of the cannulation procedure and to M. Graham for his assistance with computer analysis of RIA. This investigation was supported by Public Health Service grant HD-03803 to F.H.B. from the National Institute of Child Health and Human Development and by an NSF graduate fellowship to A.C.

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Inbreeding and Juvenile Mortality in Small Populations of Ungulates

Abstract. Juvenile mortality of inbred young was higher than that of noninbred young in 15 of 16 species of captive ungulates. In 19 of 25 individual females, belonging to ten species, a larger percentage of young died when the female was mated to a related male than when she was mated to an unrelated male.

An ever increasing number of the world's ungulate species exist only in relatively small populations in which some degree of inbreeding will inevitably occur. Extensive studies of laboratory and domestic mammals and birds indicate that inbreeding leads, in the majority of cases, to increased mortality in young animals and reduced fertility in

adults (1-3). Inbred animals are usually "less able to cope with their environment than are noninbred animals" (2, p. 215) and are often more susceptible to various diseases and environmental stresses (3, 4). The limited data from natural populations suggest that close inbreeding has the same deleterious consequences in the wild (5).

Table 1. Juvenile mortality in inbred and noninbred young.

Species	Non-inbred young	In-bred young	N	χ^2 test		Sign test*
				χ^2	P	
<i>Elephas maximus</i> (Indian elephant)						
Lived	11	2	19			
Died	2	4		4.997	.025†	+
<i>Equus burchelli</i> (zebra)						
Lived	20	3	32	.413	.528†	+
Died	7	2				
<i>Choeropsis liberiensis</i> (pygmy hippopotamus)						
Lived	139	23	235	17.28	.000†	+
Died	45	28				
<i>Muntiacus reevesi</i> (muntjac)						
Lived	18	12	40	1.212	.270	+
Died	4	6				
<i>Cervus eldi thamin</i> (Eld's deer)						
Lived	13	0	24	11.679	.001†	+
Died	4	7				
<i>Elaphurus davidianus</i> (Père David's deer)						
Lived	15	19	39	.030	.857	+
Died	2	3				
<i>Rangifer tarandus</i> (reindeer)						
Lived	19	9	50	2.538	.107	+
Died	10	12				
<i>Giraffa camelopardalis</i> (giraffe)						
Lived	11	2	19	2.537	.107	+
Died	3	3				
<i>Tragelaphus strepsiceros</i> (kudu)						
Lived	10	8	25	.005	.941	-
Died	4	3				
<i>Tragelaphus spekei</i> (sitatunga)						
Lived	15	31	75	9.012	.006†	+
Died	1	28				
<i>Hippotragus niger</i> (sable)						
Lived	18	3	32	8.183	.005†	+
Died	4	7				
<i>Oryx dammah</i> (scimitar-horned oryx)						
Lived	35	0	42	28.378	.000†	+
Died	2	5				
<i>Connochaetes taurinus</i> (wildebeest)						
Lived	6	29	48	.680	.419	+
Died	1	12				
<i>Madoqua kirki</i> (dik-dik)						
Lived	10	7	32	.473	.499	+
Died	7	8				
<i>Gazella dorcas</i> (Dorcas gazelle)						
Lived	36	17	92	9.288	.003†	+
Died	14	25				
<i>Capricornis crispus</i> (Japanese serow)						
Lived	52	27	135	10.585	.002†	+
Died	21	35				

*For the sign test, + = juvenile mortality higher in inbred than noninbred young ($P = .0003$). †Significant at .05 level; one degree of freedom in all cases; probabilities are rounded to three places.

Table 2. Breeding success of individual females which were mated to both unrelated and related males.

Species	Female (No.)	Mating with unrelated male		Mating with related male		Sign test*
		Births (No.)	Juvenile deaths (No.)	Births (No.)	Juvenile deaths (No.)	
Pygmy hippopotamus	61	1	0	9	8	+
	87	7	0	6	2	+
	102	3	1	3	2	+
	112	10	3	1	1	+
Muntjac	101,432	10	1	3	1	+
	34,847	8	0	2	0	0
	M00,510	1	1	4	2	-
Eld's deer	M00,391	1	0	2	2	+
	M00,281	1	1	3	3	0
Père David's deer	M00,346	1	0	3	1	+
Reindeer	M00,029	2	0	3	2	+
Oryx	M00,262	4	0	1	1	+
	M00,263	4	0	1	1	+
Wildebeest	28-375A	5	0	2	2	+
Dik-dik	M00,540	4	1	1	1	+
	M00,901	1	0	1	1	+
Dorcas gazelle	28,147-B	10	5	3	1	-
	28,918	8	0	11	6	+
	30,168	5	3	6	5	+
Japanese serow	TYM-1	9	1	2	0	-
	KYT-7	6	2	1	1	+
	JSC-2a	2	1	4	4	+
	JSC-2d	1	1	2	2	0
	OMC-12	6	2	1	1	+
	KOB-1cc	2	0	2	1	+

*For the sign test, + = juvenile mortality higher when mated with related male ($P = .0082$).

Although the deleterious effects of inbreeding are well known to geneticists and students of animal husbandry, they have been ignored, or even denied, by many workers in conservation and wildlife management. In an article on the captive breeding of rare and threatened deer, Whitehead (6) recently expressed the view of many skeptics: "Adverse comment about the ill-effects of inbreeding is, in my opinion, often exaggerated, and provided the area is well looked after and not overstocked, there should be no harmful effects. . . . No living mammal could be more inbred than the Père David's deer, for the whole world stock is derived from the initial Woburn stock, yet it seems to have changed little over the years."

Skepticism as to the harmful effects of inbreeding in the majority of ungulates probably stems from a number of sources: the existence of a few successful highly inbred species—such as the Père David's deer—ignorance of the severe problems with increased juvenile mortality and decreased fertility encountered during the development of the modern inbred strains of laboratory animals (7) and livestock breeds (8), and the rarity of recorded instances of deleterious effects of inbreeding in captive exotic species (9, 10). Seal (11) has suggested that the rarity of such reports in-

dicates not that exotic species tend to be more resistant to the harmful effects of inbreeding than common laboratory and domestic animals, but only that few zoos have maintained and analyzed adequate records.

We report here on the relation between inbreeding and juvenile mortality in 16 species of captive ungulates (12). Because of the small sample sizes, we compared only two levels of inbreeding: "noninbred," which included all young with unrelated parents, and "inbred," which included all young with an inbreeding coefficient greater than zero (13). Of the inbred young for which it was possible to calculate an inbreeding coefficient, 75 percent had inbreeding coefficients of 0.25 or more. Young that survived 6 months or more were considered to have "lived." The "died" category consisted of all young surviving less than 6 months, including stillbirths and those born prematurely.

The number of inbred and noninbred young that lived and died in each of the 16 species is shown in Table 1. Juvenile mortality was significantly higher in inbred than noninbred young in the four species with the largest sample sizes (pygmy hippopotamus, Japanese serow, Dorcas gazelle, and sitatunga) and four species in which the sample size was small but the mortality of inbred young

was very high (elephant, Eld's deer, sable, and oryx). The increased mortality rate of inbred young in the four species with the largest sample sizes ranged from a low of 28 percent in the Japanese serow to a high of 41 percent in the sitatunga. Inbred young had a higher mortality in 15 of 16 species ($P = .0003$, one-tailed sign test), which suggests that increased juvenile mortality in inbred young is a general phenomenon in ungulates and that the failure to show a significant difference by the chi square test in some cases may be due to an insufficient sample size per cell. In 19 of 25 individual females, belonging to ten species, a larger percentage of young died when the female was mated to a related male than when she was mated to an unrelated male (Table 2) ($P = .008$, one-tailed sign test).

We have not yet analyzed most of our data with respect to the many other variables that might influence juvenile mortality, such as birth season, management improvements, birth order of the young, and possible differences between wild- and captive-born females. However, a detailed analysis of the data on the species with the largest sample size of those for which we had medical records (Dorcas gazelle) showed that none of these significantly affected the high mortality rates of inbred young (10). Furthermore, causes of death in inbred and noninbred gazelle calves were strikingly different. Once past the immediate postnatal period, noninbred calves were remarkably sturdy. Only five died after the age of 4 days, all of traumas sustained during capture or transport. Inbred calves often succumbed to inanition and a variety of miscellaneous medical problems and infections not found in noninbred calves.

Our results support Seal's (11) claim that deleterious effects of inbreeding are widespread in captive populations of exotic animals and have remained unrecognized only because the majority of zoos have not maintained detailed records. To date, conservationists have paid relatively little attention to the problem of preserving genetic variability in small populations of ungulates, whether these are captive breeding stocks, translocated or reintroduced populations, or small populations in isolated reserves. The degree of inbreeding depression in a small ungulate population of a given size presumably varies with many factors, such as the mating system of the species, its genetic load, and the length of time the population has been genetically isolated (14). However, because inbreeding has been shown to reduce viability and fertility in such taxonomically distant orga-

nisms as insects (3, p. 87) and plants (3, p. 6), it seems reasonable to predict that these effects may be expected in the majority of normally outbreeding ungulate species. The evidence that inbreeding often leads to increased juvenile mortality and other deleterious effects in ungulates is at hand and the time has come to institute sound genetic management of small ungulate populations wherever practicable, without waiting for evidence of such effects in each species or population.

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12. The elephant data were obtained from the Washington Park Zoo in Portland, Ore., and the Japanese serow data from Atushi Komori, keeper of the studbook for this species. The sitatunga data were taken from a pedigree published by E. M. Lang [*Zool. Gart. N.F.* **49**, 8-16 (1978)] and the pygmy hippopotamus data from the published studbook [E. M. Lang, *Das Zwergflüsspferd* (Ziemsen, Wittenberg, Lutherstadt, 1975)]. Part of the sable data were obtained from the Baltimore Zoo. Additional sable data and all the data on the 11 other species were collected from

the records of the National Zoological Park (N.Z.P.), Washington, D.C.

13. Inbreeding coefficients (F) were calculated by hand from the formula $F_x = \frac{1}{2} \sum [(1/2)^n (1 + F_a)]$ (2, p. 240). We assumed that the individuals used to found a population were unrelated, although we knew that this assumption was unjustified in some cases. Unless we knew the manner in which individuals subsequently obtained from outside sources were related to existing stock, we assumed they were unrelated. In some cases, it was not possible to calculate an exact inbreeding coefficient although we knew it must be greater than zero.
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Relatedness and Inbreeding Avoidance: Counterplays in the Communally Nesting Acorn Woodpecker

Abstract. *Acorn woodpeckers* (*Melanerpes formicivorus*) live in family groups within which more than one female may lay eggs communally in a single nest. Communally nesting females are usually closely related and share evenly in nesting activities. Although birds of either sex may breed in their natal territory, reproductive inhibition of offspring by the presence of their parent of the opposite sex and dispersal by unisexual sibling units ensure that inbreeding between close relatives is rare.

True communal nesting, in which more than one female regularly lays eggs in the same nest, is known from some ten species of birds (1). In none of these has either the genetic relatedness among such females or the consequences of communal nesting on amount of inbreeding been identified. We report such data for the acorn woodpecker. These data are difficult to gather and some of our sample sizes are small; but the results bring out significant components of social dynamics acting to prevent inbreeding and needing attention in studies of all cooperative breeding birds.

In California, the acorn woodpecker typically lives in permanently territorial family groups of 2 to 15 birds (2). Only a single nest is attended at any one time by a group, and most or all group members help to incubate and feed the young. Unlike many group-living species, either males or females may breed in their natal territory (3), thus apparently presenting unusually great opportunities for inbreeding among close relatives.

As part of a continuing long-term study of the social behavior of this species at the Hastings Natural History Reservation, we recorded intergroup transfers of marked birds and clutch size in relation to group composition (3). On the basis of the deposition of two eggs on each of one or more days in a nest (4), we found that two females were nesting together in at least 3 of 27 group breeding efforts in which the nest was found before hatching and two or more females were known to be members of the group. Evidence from clutches of groups with differing compositions permits an analysis of the restrictions placed on reproduction by females and the conditions under which more than one female may lay eggs in a nest. Our results suggest that (i) large sets of eggs are the result of true communal nesting rather than intraspecific nest parasitism by females from outside the group, (ii) females do not breed in their natal group as long as their known or presumed father is still in the group, and (iii) communally nesting fe-

Table 1. Relatedness of acorn woodpeckers immigrating in unisexual units of either sex.

Origin	Number of units	Number of individuals
Siblings from the same group	8 (42 percent)	18 (40 percent)
Birds from the same group, two of which were known siblings*	3 (16 percent)	9 (20 percent)
Birds from the same group, one or none of which was known to have been born there*	7 (37 percent)	16 (36 percent)
Birds from different groups	1 (5 percent)	2 (4 percent)
Total	19 (100 percent)	45 (100 percent)

*These units are also likely to have been siblings.