

Estimates of Lethal Equivalents and the Cost of Inbreeding in Mammals

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Abstract: *The costs of inbreeding in natural populations of mammals are unknown despite their theoretical importance in genetic and sociobiological models and practical applications in conservation biology. A major cost of inbreeding is the reduced survival of inbred young. We estimate this cost from the regression of juvenile survival on the inbreeding coefficient using pedigrees of 40 captive mammalian populations belonging to 38 species.*

The number of lethal equivalents ranged from -1.4 to 30.3, with a mean of 4.6 and a median of 3.1. There was no significant difference between populations founded with wild-caught individuals, a mixture of wild-caught and captive-born individuals, and individuals of unknown origin. The average cost of a parent-offspring or full sibling mating was 0.33, that is, mortality was 33% higher in offspring of such matings than in offspring of unrelated parents. This is likely to be an underestimate.

Resumen: *Los costos de procreación en consanguinidad en poblaciones naturales de mamíferos son desconocidos a pesar de su importancia teórica en los modelos genéticos y sociobiológicos y en sus aplicaciones prácticas para la biología de la conservación. Uno de los costos mayores de la procreación en consanguinidad es la disminución en la sobrevivencia de las crías consanguíneas. Estimamos este costo por medio de la regresión de la sobrevivencia juvenil en el coeficiente de procreación en consanguinidad utilizando pedigrís de 40 poblaciones de mamíferos en cautiverio pertenecientes a 38 especies.*

El número de equivalentes letales varió de -1.4 a 30.3, con una media de 4.6 y una mediana de 3.1. No hubo diferencia significativa entre poblaciones formadas a partir de individuos silvestres capturados, a partir de una mezcla de individuos silvestres capturados, y a partir de individuos de origen desconocido. El costo promedio del apareamiento de padre-cría o hermanos completamente consanguíneos fue de 0.33, es decir, la mortalidad fue 33% más alta en las crías de tales apareamientos que en las crías de especies no relacionadas. Es probable que este cálculo sea una subestimación.

Introduction

Many studies of laboratory, domestic, and zoo animals have documented reduced survival and fecundity of inbred young (Wright 1977; Ralls & Ballou 1983; Sausman 1984; Templeton & Read 1984). Inbreeding depression is thus a major concern in the management of small populations, and estimates of the cost of inbreeding are of considerable importance to conservation biology.

However, inbreeding can increase an individual's inclusive fitness by producing young that share more of its genome. Thus, when inbreeding has little or no genetic cost, there should be strong selective advantage for inbreeding as well as recognition and cooperation among kin (Wilson 1976; May 1979). The cost of inbreeding is therefore of theoretical importance as well.

Calculations of the total cost of inbreeding in natural populations would involve considering the effects of inbreeding on several components of fitness. However, the "cost of inbreeding" that appears in a variety of theoretical models (Dawkins 1976; Bengtsson 1978; Parker 1979; Smith 1979; Feldman & Christiansen 1984) is defined solely in terms of the survival of inbred young relative to non-inbred young. There are almost no estimates of this quantity in natural populations of mammals (Packer 1979).

We estimate this cost from pedigrees of 40 captive mammalian populations belonging to 38 species.

Methods

Morton, Crow, & Muller (1955) developed a log model for estimating the cost of inbreeding from the rate at which juvenile survival decreases with increasing amounts of inbreeding. Specifically,

$$S = e^{-(A + BF)} \quad (1)$$

where S is the proportion of individuals surviving to some age, F is the inbreeding coefficient, A is considered a measure of death due to environmental causes and the genetic damage expressed in a randomly mating population, and B is a measure of the rate at which survival decreases with increasing inbreeding.

Makov & Bittles (1986) evaluated the use of this and several other equations to estimate effects of inbreeding in humans. They found that many different models could adequately detect significant inbreeding effects; however, different models resulted in different values of A and B . Because of the limited range of inbreeding levels in available data from human populations ($F = 0-0.125$), they were unable to determine which equation most adequately modeled data on inbreeding effects in humans. They suggested that different equations could more effectively be evaluated in animal populations with wider ranges of inbreeding levels.

We evaluated the log transformed equation (1) and two other equations, using several of our largest data sets with relatively wide ranges of inbreeding levels ($F = 0-0.5$). The two additional equations were

$$S = A + B(F) \quad (2)$$

$$\arcsin\sqrt{S} = A + B(F) \quad (3)$$

where S , A , B , and F are the same values as in equation (1). Model 2 was used because it represents the simplest linear relationship between the variables. Model 3 (angular transformation) was used since it is often recommended for estimating proportions (Sokal & Rohlf 1969). Weighted least squares regression, with a small sample size correction (Templeton & Read 1984), was used to estimate the parameters for each of the models. The total percentage of variation explained by the equation (R^2) was used to evaluate which model best fitted the data.

When analyzing pedigrees of zoo animals, care must be taken to distinguish inbreeding depression from hybridity effects or "outbreeding depression" (Templeton & Read 1984; Templeton et al. 1986). We therefore carried out the analysis developed for this purpose by Templeton & Read (1984) on those pedigrees with adequate sample sizes but found no evidence of outbreeding depression (Templeton & Read 1984; unpublished data).

Inbreeding coefficients (F) were calculated for each animal in each pedigree, relative to the founders of the population. Methods for calculating F from pedigree data are given by Ballou (1983). F is the probability that the two alleles present at a given locus are "identical by descent"—that is, are derived by replication of a single allele from a common ancestor. F ranges from 0 in a non-inbred individual to 1.0 in a completely inbred (homozygous) individual (Crow & Kimura 1970). The effect of inbreeding is often less severe in individuals with inbred ancestors (Bowman & Falconer 1960; Lorenc 1980; Templeton & Read 1984), but we were unable to exclude them from the analysis because this eliminated all levels of inbreeding except $F = 0.25$ in many pedigrees.

Levels of inbreeding varied among pedigrees (Table 1). For each level of inbreeding represented in a particular pedigree, we calculated the proportion of animals that survived to a criterion age. This was 180 days for the larger species and one-half the age at sexual maturity for the smaller ones (Table 2). Ideally, studies of the relationship between inbreeding and juvenile mortality should be based upon the total mortality before reaching reproductive age (Cavalli-Sforza & Bodmer 1971), but we were unable to follow many individuals for this period because zoo animals are often transferred to other institutions before reaching reproductive age. Considering survival to a criterion age less than repro-

Table 1. Comparison of models used for estimating cost of inbreeding.

| SPECIES ^a | Maximum Inbreeding level | Comparison of R ² Values MODEL | | |
|---------------------------|-----------------------------|--|------------|------------|
| | | Log (1) | Linear (2) | Arcsin (3) |
| Short bare-tailed opossum | .328 | .80 | .79 | .77 |
| Elephant shrew | .125 | .05 | .06 | .07 |
| Golden lion tamarin | .375 | .35 | .26 | .26 |
| Greater galago | .250 | .17 | .14 | .13 |
| Maned wolf | .312 | .77 | .83 | .83 |
| Bush dog | .500 | .02 | .00 | .00 |
| Pygmy hippopotamus | .375 | .45 | .55 | .55 |
| Dorcas gazelle | .375 | .64 | .66 | .63 |

^aScientific names listed in Table 2.

ductive maturity tends to underestimate the cost of inbreeding, as inbred mortality increases more rapidly than non-inbred mortality with increasing age in some species (Ralls, Brugger, & Glick 1980; unpublished data).

Results

Table 1 shows the results of the three models applied to eight of the largest data sets. R² values were highest for the Linear model (2) in 2 populations, highest for the Arcsin model (3) in 2 populations, and highest for the log model (1) in 4 populations. As Makov and Bittles (1986) concluded, no one model was clearly better than the others; R² values ranged over only a few percentage points across the models.

The log transformed model (1) has been used extensively in the literature to estimate number of lethal equivalents and is the theoretically expected model, if it is assumed that genetic and environmental influences are independent of each other with respect to survival (Morton, Crow & Muller 1955). Use of this model also facilitates comparisons with A and B values already published in the literature. We therefore selected it for all subsequent analyses.

Estimates for A and B are shown in Table 2. Values of A ranged from 0.03 to 1.11 with a mean of 0.33 and a median of 0.32. Values for B ranged from -0.68 to +15.16, with a mean of +2.33 and a median of +1.57 (Fig. 1). Of the 40 populations, 36 had positive slopes, which clearly indicates an overall trend towards higher levels of juvenile mortality with increasing inbreeding coefficients (Sign test, $P < .001$). This relationship was statistically significant—that is, the slope of the line was significantly greater than zero—in only 9 (23%) of the populations. However, most of our sample sizes were small and distributed over only a few levels of inbreeding. The statistical power to detect slopes significantly greater than zero was therefore limited. Considering only those populations in which the relationship between inbreeding and survival is significant would be

likely to greatly overestimate the average cost of inbreeding in mammals. Limiting the analysis to only those species with relatively large data sets increases the power of the statistical comparisons but reduces the number of species that can be analyzed. Only 10 species had more than five levels of inbreeding and total sample sizes over 100. Six of these 10 had slopes significantly different from zero; the average B value was 1.98, with a median of 1.64. These B values did not differ significantly from those in the overall data set (Mann-Whitney U test, $P > 0.05$).

The distributions of B by order are shown in Figure 2. Median values were between one and two except for the Carnivora. There were no statistically significant differences between average B values in populations founded with wild-caught individuals ($\bar{x} = 2.57$, $n = 18$), a mixture of wild-caught and captive individuals ($\bar{x} = 2.42$, $n = 11$), and individuals of unknown origin ($\bar{x} = 1.95$, $n = 10$) (Kruskal-Wallis Test, $P = 0.88$).

The number of lethal equivalents per gamete lies between B and A but is usually very close to B (Cavalli-Sforza & Bodmer 1971; Crow & Kimura 1970). The number per zygote or individual is twice the number per gamete, thus our estimates of the average number of lethal equivalents per individual are twice the values of B in Table 2, with a mean of 4.6 and a median of 3.1. We estimated the cost of inbreeding for matings between first-degree relatives (parents and their offspring or full siblings) by solving equation (1) for each species using $F = 0$ and $F = 0.25$ to obtain the predicted survivorship at these levels of inbreeding. The cost of inbreeding (i) at $F = 0.25$ is then equal to

$$i = 1 - \frac{\text{Survivorship at } F = 0.25: e^{-(A+.25B)}}{\text{Survivorship at } F = 0: e^{-A}}$$

$$= 1 - e^{-.25B}. \quad (4)$$

The average cost of inbreeding between first degree relatives, calculated by averaging the costs across all populations, was 0.33 (Table 2). Solving equation (4)

Table 2. The cost of inbreeding in 40 mammalian populations.

| TAXON | Survival to Age (Days) | N | Founder ^a Type | No. of Inbred Levels | Model Estimates | | Model R ² | Cost of Inbreeding ^c at F = 0.25 | Data Source |
|--|------------------------|-----|---------------------------|----------------------|-----------------|-------------------|----------------------|---|---|
| | | | | | A | B | | | |
| MARSUPIALIA | | | | | | | | | |
| Short bare-tailed opossum (<i>Monodelphis domestica</i>) | 75 | 251 | W | 6 | 0.03 | 0.43 ^b | 0.80 | .10 | National Zoo |
| Parma wallaby (<i>Macropus parma</i>) | 180 | 17 | W | 5 | 0.32 | 1.69 | 0.47 | .34 | National Zoo |
| INSECTIVORA | | | | | | | | | |
| Elephant shrew (<i>Elephantulus rufescens</i>) | 21 | 218 | W | 7 | 0.28 | 2.12 | 0.05 | .41 | National Zoo |
| PRIMATES | | | | | | | | | |
| Black spider monkey (<i>Ateles fusciceps robustus</i>) | 180 | 23 | W | 3 | 0.23 | 2.22 | 0.88 | .43 | National Zoo |
| Saddle-backed tamarin (<i>Saguinus fuscicollis</i>) | 180 | 233 | U | 2 | 1.11 | 1.86 | — | .37 | Monell Chemical Senses Center |
| Illiger's saddle-backed tamarin (<i>Saguinus f. illigeri</i>) | 180 | 406 | U | 4 | 0.40 | 7.92 | 0.40 | .82 | Rush-Presbyterian St. Luke's Medical Center |
| Golden lion tamarin (<i>Leontopithecus r. rosalia</i>) | 180 | 974 | W | 18 | 0.54 | 2.15 ^b | 0.35 | .42 | 1984 Studbook |
| Ring-tail lemur (<i>Lemur catta</i>) | 180 | 53 | M | 4 | 0.34 | 0.13 | 0.01 | .03 | Oregon Primate Research Center |
| Black lemur (<i>Lemur macaco</i>) | 180 | 43 | W | 3 | 0.52 | 2.78 | 0.87 | .50 | Oregon Primate Research Center |
| Brown lemur (<i>Lemur fulvus</i>) | 180 | 136 | M | 6 | 0.32 | 9.17 ^b | 0.94 | .90 | Oregon Primate Research Center |
| Greater galago (<i>Galago c. crassicaudatus</i>) | 180 | 251 | M | 29 | 0.45 | 1.69 ^b | 0.17 | .34 | Oregon Primate Research Center |
| Melanotic galago (<i>Galago c. argentatus</i>) | 180 | 54 | M | 4 | 0.36 | 0.48 | 0.19 | .11 | Oregon Primate Research Center |
| Crab-eating macaque (<i>Macaca fascicularis</i>) | 180 | 237 | U | 3 | 0.37 | 0.29 | 0.56 | .07 | New England Primate Research Center |
| Celebes black ape (<i>Macaca nigra</i>) | 180 | 86 | U | 3 | 0.38 | 2.84 | 0.70 | .51 | Oregon Primate Research Center |
| Chimpanzee (<i>Pan troglodytes</i>) | 180 | 247 | U | 4 | 0.35 | 1.05 | 0.67 | .23 | Yerkes Primate Center |
| RODENTIA | | | | | | | | | |
| Climbing rat (<i>Tylomys nudicaudus</i>) | 45 | 49 | U | 5 | 0.23 | -0.14 | 0.02 | -.04 | National Zoo |
| Wied's red-nosed rat (<i>Wiedomys pyrrhorhinos</i>) | 30 | 23 | W | 2 | 0.05 | 15.16 | — | .98 | National Zoo |
| Rock cavy (<i>Kerodon rupestris</i>) | 90 | 132 | U | 3 | 0.12 | 0.77 | 0.87 | .18 | National Zoo |
| Salt-desert cavy (<i>Dolichotis salinicola</i>) | 90 | 17 | W | 2 | 0.08 | 7.21 | — | .34 | National Zoo |
| Acouchi (<i>Myoprocta pratti</i>) | 135 | 36 | U | 5 | 0.30 | 2.20 | 0.17 | .42 | National Zoo |
| Boris (<i>Octodontomys gliroides</i>) | 75 | 53 | U | 6 | 0.26 | 1.15 | 0.33 | .25 | National Zoo |
| Punare (<i>Cercomys cunicularus</i>) | 60 | 161 | W | 4 | 0.10 | 0.94 ^b | 0.91 | .21 | National Zoo |
| CARNIVORA | | | | | | | | | |
| Maned wolf (<i>Chrysocyon brachyurus</i>) | 180 | 338 | M | 4 | 0.52 | -0.68 | 0.77 | -.19 | 1983 Studbook |
| Bush dog (<i>Speothos venaticus</i>) | 180 | 176 | W | 9 | 0.54 | 0.24 | 0.02 | .06 | 1983 Studbook |
| Sumatran tiger (<i>Panthera tigris sumatrae</i>) | 180 | 427 | M | 12 | 0.49 | 0.01 | 0.00 | .003 | 1983 Studbook |
| PERISSODACTYLA | | | | | | | | | |
| Zebra (<i>Equus burchelli</i>) | 180 | 50 | U | 2 | 0.30 | 1.56 | — | .32 | National Zoo |
| ARTIODACTYLA | | | | | | | | | |
| Pygmy hippopotamas (<i>Choeropsis liberiensis</i>) | 180 | 419 | W | 12 | 0.33 | 1.59 ^b | 0.45 | .33 | 1982 Studbook |

Table 2. Continued

| TAXON | Survival to Age (Days) | N | Founder ^a Type | No. of Inbred Levels | Model Estimates | | Model R ² | Cost of Inbreeding ^c at F = 0.25 | Data Source |
|--|------------------------|-----|---------------------------|----------------------|-----------------|-------------------|----------------------|---|------------------------|
| | | | | | A | B | | | |
| Reeves muntjac (<i>Muntiacus reevesi</i>) | 180 | 75 | M | 9 | 0.19 | 1.20 | 0.37 | .26 | National Zoo |
| Eld's Deer (<i>Cervus eldi thamin</i>) | 180 | 24 | M | 2 | 0.31 | 7.57 | — | .85 | National Zoo |
| Pere David's Deer (<i>Elaphurus davidianus</i>) | 180 | 39 | C | 7 | 0.17 | 0.63 ^b | 0.74 | .15 | National Zoo |
| Reindeer (<i>Rangifer tarandus</i>) | 180 | 50 | W | 4 | 0.32 | 4.20 | 0.71 | .65 | National Zoo |
| Giraffe (<i>Giraffa camelopardalis</i>) | 180 | 19 | W | 2 | 0.29 | 2.24 | — | .43 | National Zoo |
| Kudu (<i>Tragelaphus strepsiceros</i>) | 180 | 25 | W | 2 | 0.37 | -0.03 | — | -.01 | National Zoo |
| Bongo (<i>Tragelaphus eurycerus</i>) | 180 | 74 | W | 3 | 0.23 | -0.55 | 0.74 | -.15 | 1984 Studbook |
| Gaur (<i>Bos gaurus</i>) | 180 | 182 | W | 6 | 0.18 | 0.51 | 0.36 | .12 | Hinz & Foose, 1982 |
| Scimitar-horned oryx (<i>Oryx dammah</i>) | 180 | 81 | M | 2 | 0.09 | 4.63 | — | .69 | National Zoo |
| Wildebeest (<i>Connochaetes taurinus</i>) | 180 | 42 | W | 11 | 0.33 | 0.28 | 0.02 | .07 | National Zoo |
| Dik-dik (<i>Madoqua kirki</i>) | 180 | 20 | M | 3 | 0.80 | 0.59 | 0.12 | .14 | National Zoo |
| Dorcas gazelle (<i>Gazella dorcas</i>) | 180 | 143 | M | 15 | 0.34 | 1.85 ^b | 0.64 | .37 | National Zoo |
| Spekes gazelle (<i>Gazella speket</i>) | 30 | 64 | W | 5 | 0.22 | 3.08 ^b | 0.92 | .54 | Templeton & Read, 1983 |
| | | | Mean: | | 0.33 | 2.33 | | 0.33 | |
| | | | Median: | | 0.32 | 1.57 | | 0.33 | |
| | | | Lower Quartile: | | 0.23 | 0.45 | | 0.09 | |
| | | | Upper Quartile: | | 0.39 | 2.81 | | 0.47 | |

^a Founder Type: W = All founders wild-caught.

C = Founders captive-born.

M = Founders were a mix of wild-caught and captive-born.

U = Source of founders unknown.

^b B (slope) significantly different than zero at the 0.05 level.

^c Cost of inbreeding for F = 0.25: $= 1 - \left[\frac{\text{Predicted inbred survival: } e^{-(A+.25B)}}{\text{Predicted non = inbred survival: } e^{-A}} \right] = 1 - e^{-.25B}$.

using the average B value (2.3) results in a cost of inbreeding of 0.44. However, the statistic of interest here is the estimate of the expected value of the cost of inbreeding rather than the cost of inbreeding calculated from the expected value of B. We therefore base our discussion on an average cost of inbreeding of 0.33. The distribution of the cost of inbreeding between first degree relatives is shown in Figure 3.

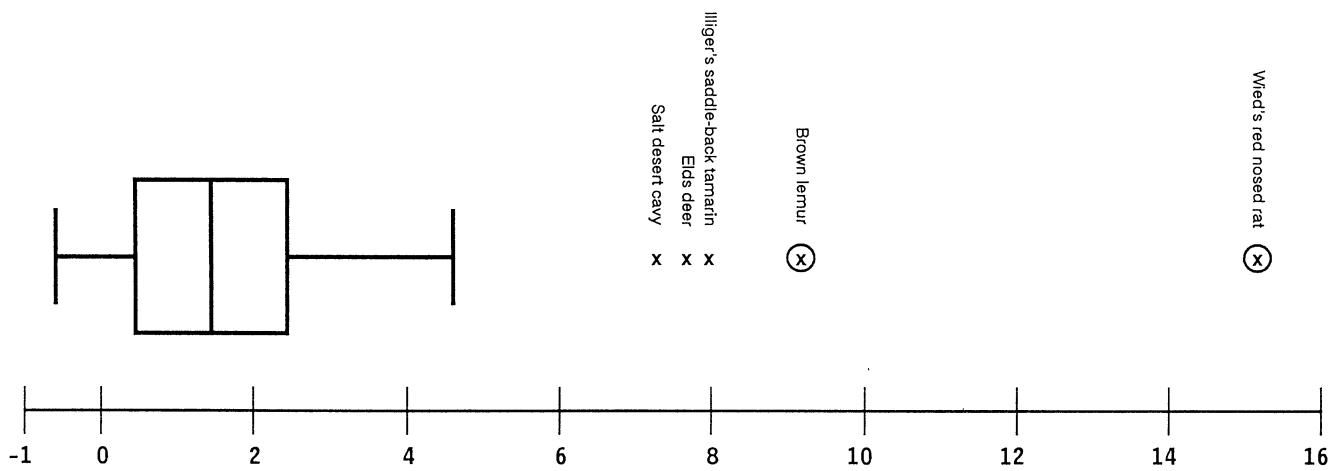
Discussion

The costs of inbreeding varied widely among captive populations. This is not surprising since one would expect populations to differ in their level of susceptibility to inbreeding. However, in many cases, the models fit the data very poorly and only a small proportion of the variance was explained. These variable results probably reflect the heterogeneous data used for the analysis. The available data for the populations surveyed differed in sample size and the range and number of levels of inbreeding. Nevertheless, these results do provide data on

the costs of inbreeding and number of lethal equivalents in a wide variety of captive populations and allow analyses of general trends and patterns.

The median number of estimated lethal equivalents for the captive mammalian populations we examined was 3.1. This figure is similar to estimates for other animal populations. Humans (May 1979), *Drosophila* (Dobzhansky 1970), and the great tit, *Parus major* (Bulmer 1973), are thought to have about two lethal equivalents per individual, and the Japanese quail, *Coturnix coturnix japonica*, is thought to have about 3.4 (Sittmann, Abplanalp & Fraser 1986). Our estimates for captive carnivores, although based on only three populations, were quite low. More carnivore populations should be studied to determine if this is characteristic of the order or unique to the data sets we examined.

May (1979), assuming the number of lethal equivalents in humans was 2.2, estimated the cost of breeding in humans at F = 0.25 to be .42. However, his equation for calculating the inbreeding cost contained an error. The correct cost, based on formula (4), is .24. This es-



B (Rate at which Survival Decreases with Inbreeding)

Figure 1. Box plots of B, a measure of the rate at which survival decreases with increasing inbreeding, for 40 mammalian populations. The median (middle vertical line in box), upper and lower quartiles (left and right ends of box), upper and lower inner fences (vertical lines), outlying values (x), and values beyond the outer fences (⊗) are shown (Hoaglin, Mosteller, & Tukey 1983).

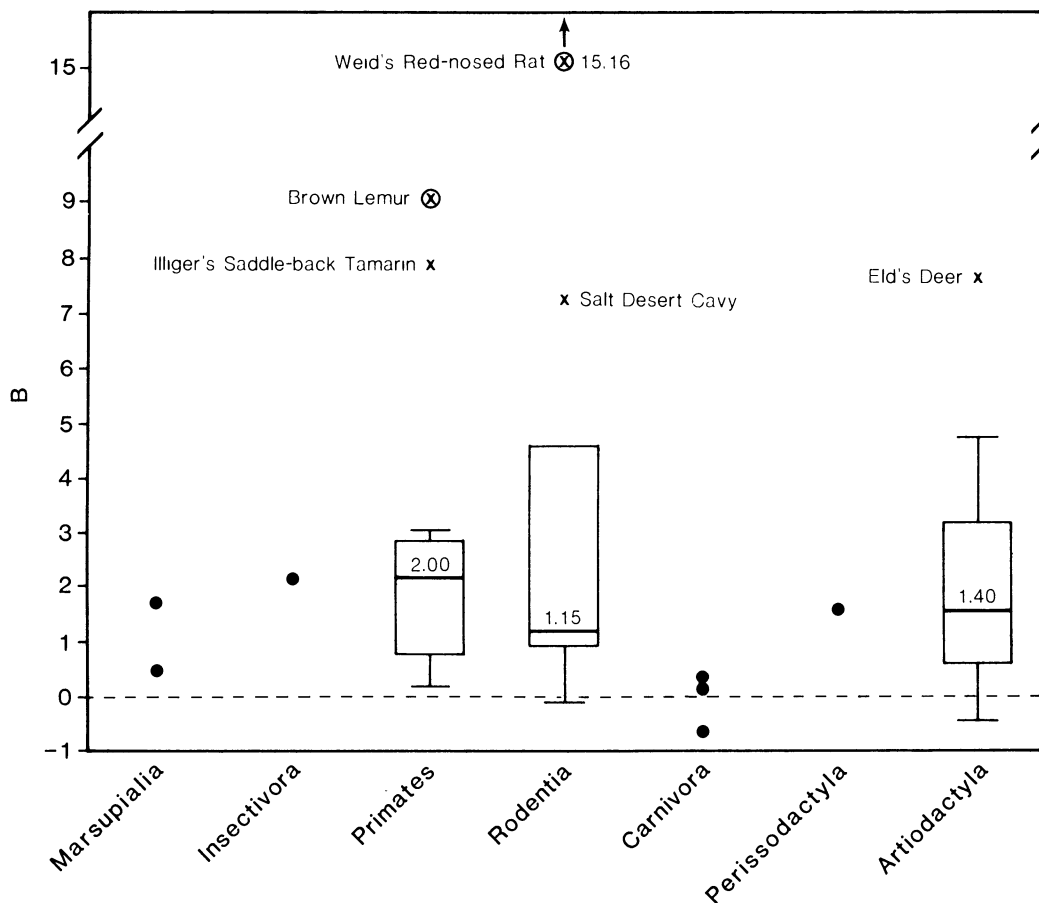


Figure 2. Box plots of B across 40 mammalian populations by order. Median effects (middle horizontal line in box), upper and lower quartiles (upper and lower ends of boxes), upper and lower inner fences (horizontal lines), outlying values (x), and values beyond the outer fences (⊗) are shown for the distribution of B in primates, rodents, and artiodactyls. Results for individual populations in other orders are shown by solid dots.

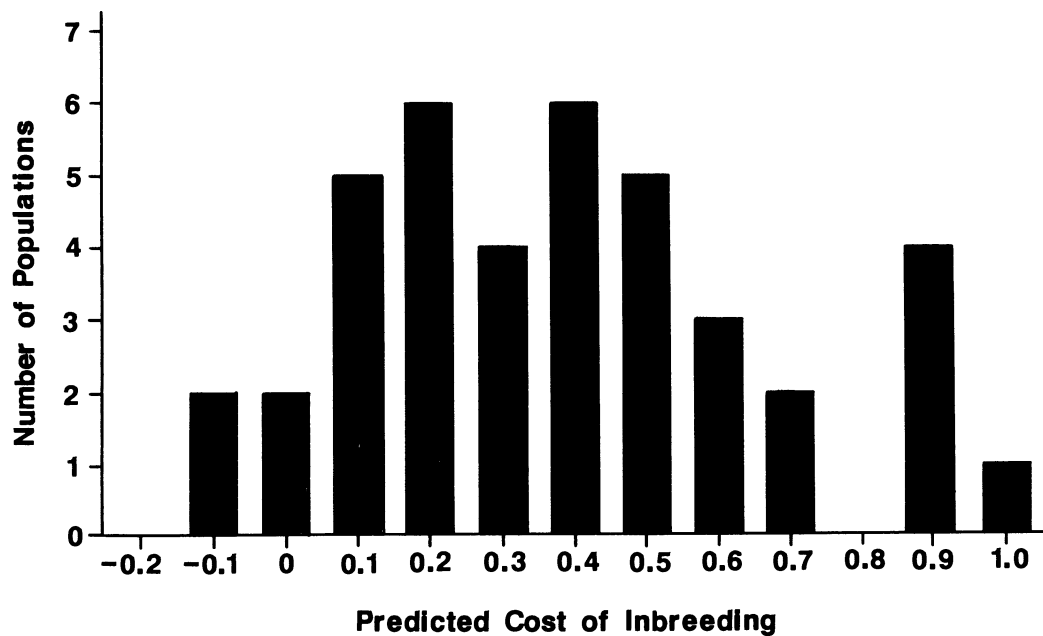


Figure 3. Distribution of the predicted cost of inbreeding in matings resulting in young with an inbreeding coefficient of 0.25 (i.e., matings between parents and offspring or full siblings) for 40 mammal populations.

estimate is slightly lower than the average .33 cost of inbreeding found in our mammal populations.

The total costs of inbreeding in natural populations are probably considerably higher than our estimates. First, our estimate of the cost based on only one component of fitness (survival of young) is probably low. We were unable to count early embryonic deaths, exclude individuals with inbred ancestors, and follow individuals until the age of reproductive maturity. Furthermore, mortality rates of inbred young may be higher in natural populations, because many weak young that might die in the wild survive in captivity with the assistance of veterinary care. Second, there are likely to be additional costs of inbreeding in other components of fitness, such as litter size in species that normally bear multiple young and a reduction in fecundity of the inbred young that do survive to reproductive age (Wright 1977). (The reported higher recruitment rate of inbred young in the great tit (van Noordwijk & Scharloo 1981) is not supported by the data (Greenwood & Harvey 1982).) Third, inbred individuals with low levels of heterozygosity may be highly susceptible to viral epidemics (O'Brien et al. 1985).

Considering only the cost of inbreeding relative to the gain in inclusive fitness due to inbreeding, theory suggests that females should not mate with their fathers or sons unless the cost of inbreeding is less than .33 (Smith 1979). Although this is a highly oversimplified model, our data suggest that the cost of inbreeding in mammals is usually high enough (mean = .33) that females should not mate with their closest relatives. The limited data on the frequency of such matings in natural

populations of mammals agree with this prediction. Estimates based on observations of identifiable individuals during long-term field studies range from zero to 2% in 9 of 14 well-studied mammalian populations, and the highest documented frequency is 5.5% (Ralls, Harvey & Lyles 1986).

Estimates of the cost of inbreeding also have important applications to conservation biology. The effects of the accelerated rate of inbreeding in small populations, in both captivity and the wild, can potentially drive a population towards extinction (Gilpin & Soulé 1986). The susceptibility of most small populations of conservation interest to elevated levels of inbreeding is unknown, and predicting the degree to which mortality may be increased as a result of inbreeding is impossible. The results presented here provide estimates of the general relationship between the rates of inbreeding and juvenile mortality in a large variety of captive mammal populations and will be useful in developing conservation management programs for small populations (Ballou, in press). Unfortunately, however, our estimates of the cost of inbreeding for individual populations varied greatly and were not clustered near the mean value. Thus, the severity of inbreeding effects in any unstudied mammalian population is quite likely to differ from that predicted by models based on average values.

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