

DEMOGRAPHIC CONSEQUENCES OF INBREEDING IN  
REMNANT POPULATIONS

L. SCOTT MILLS\*† AND PETER E. SMOUSE‡

\*Biology Department, University of California, Santa Cruz, California 95064; †Center for Theoretical and Applied Genetics, Cook College, Rutgers University, New Brunswick, New Jersey 08903-0231

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**Abstract.**—Although traditional population fragmentation theory and management has been strongly oriented toward concerns arising from inbreeding depression, recent papers suggest that small populations will be eliminated by demographic and/or environmental events before inbreeding becomes a problem. We explore the interaction between these factors by developing a stochastic, discrete time Leslie model that incorporates inbreeding depression. We model small population dynamics with three realistic demographic schedules: low growth rate "ungulates," medium growth rate "felids," and high growth rate "rodents," examining the impact of survival and fertility depression commensurate with inbreeding effects reported in the literature. Focusing on the first few generations after habitat fragmentation and isolation, we find that (a) high growth rate populations are affected only by strong inbreeding depression, but low growth rate populations are extremely vulnerable to even minor inbreeding depression; (b) vulnerability to extinction is affected more by survival depression than by fecundity depression; and (c) reductions in the sex ratio exacerbate inbreeding accumulation and hence extinction rate. Counter to the current fashion, which downplays the importance of inbreeding in stochastic environments, we conclude that, while inbreeding depression is not necessarily the primary cause of extinction, it can be critical.

When habitat alteration fragments a population into isolated subunits, the probability of demic extinction is a function of both deterministic and stochastic factors; stochastic causes are traditionally categorized as being either genetic (inbreeding) or demographic and/or environmental (Shaffer 1981; Gilpin and Soulé 1986). Population fragmentation theory and management has focused strongly on genetic models, on the premise that inbreeding accumulation will reduce fitness and accelerate extinction of small populations (Soulé and Wilcox 1980; Schonewald-Cox et al. 1983; Ewens 1990). In response to a perceived overemphasis on inbreeding depression as a cause of extinction, however, several recent papers indicate that small isolated populations may not persist long enough for inbreeding to be a problem, because they will first be eliminated by random demographic and/or environmental events (e.g., Schwartz et al. 1986; Dawson et al. 1987; Lande 1988; Pimm et al. 1988, 1989). Attention has thus begun to shift away from inbreeding depression and toward demographic and environmental stochasticity.

† Address correspondence to L. Scott Mills, Department of Fisheries and Wildlife, University of Idaho, Moscow, Idaho 83844. E-mail: smills@uidaho.edu.

The dichotomy between genetic and ecological views of extinction is useful as a heuristic device, emphasizing the multiple causes of vulnerability, but it does not formally accommodate the interaction between genetic, demographic, and environmental stochasticity (Lande 1988). Close inbreeding is strongly implicated in decreased demographic vital rates (see, e.g., Mitton and Grant 1984; Wildt et al. 1987), and inbreeding can have negative demographic consequences in small populations (Frankel and Soulé 1981; Allendorf and Leary 1986; Soulé 1987). Because the probability of stochastic extinction is largely a function of how small the population becomes and how long it stays small, the critical issue is the impact of inbreeding depression on the population growth rate ( $\lambda$ ) (Senner 1980; Soulé and Mills 1992). An explicit connection between inbreeding depression and stochastic demographic and/or environmental extinction is critical to any discussion of viable populations and to the management of natural reserves (Lande 1988; Lacy 1992).

To determine the potential impact of inbreeding on the survival of small, stochastically vulnerable populations, we incorporate inbreeding depression into a density-independent, discrete time Leslie matrix model. We then model the short-term dynamics of mammalian populations with inbreeding costs commensurate with those reported in the literature, considering a range of  $\lambda$  values, initial population sizes, and inbreeding costs.

#### POPULATION GROWTH WITH INBREEDING DEPRESSION

##### *The Leslie Matrix Projection Model*

We begin with a single-sex, discrete time Leslie projection matrix, composed of survival and reproduction rates. Two-sex projection models exist (see Pollak 1990), but they are unwieldy for our problem, so we modify the classic single-sex (female dominant) model instead. We follow Caswell's (1989) approach for a birth pulse population with censusing just prior to breeding, dividing a continuous age distribution into a number,  $K$ , of discrete age classes of equal duration:  $i = 1, 2, \dots, K$ . The population projection interval is of the same duration as the age class width. All individuals in the oldest age class,  $K$ , die by the end of the interval; for the other age classes, age-specific survival rate,  $P_i$ , is the probability of survival into the next age class ( $i + 1$ ) in the next time interval. The  $P_i$  ( $i = 1, \dots, K - 1$ ) make up the principal subdiagonal of the projection matrix,  $\mathbf{X}$ . The probability of a newborn's surviving from birth until counted in the first age class at its first census is  $P_0$ , assumed to be the same for infants born to mothers of all age classes. Age-specific fertilities make up the top row of the projection matrix,  $\mathbf{X}$ , such that the  $i$ th element includes both fecundity—the number of females born to mothers of the  $i$ th age class ( $M_i$ )—and the survival of those newborns into the first age class ( $P_0$ ). The recurrence relation for population change is thus

$$\mathbf{N}(t + 1) = \mathbf{X}\mathbf{N}(t), \quad (1)$$

where  $\mathbf{N}(t)$  is a column vector with elements  $N_1(t), N_2(t), \dots, N_K(t)$ ;  $N_i(t)$  is the number of females in age class  $i$  at time  $t$ ; and  $\mathbf{N}(t + 1)$  is the corresponding

vector for the next time step. The population growth rate  $\lambda$  is the largest real, positive eigenvalue of the projection matrix  $X$ .

### *Inbreeding Depression and Fitness*

We incorporate inbreeding costs into the demographic vital rates by modifying the classic genetic load formulation of Morton et al. (1956), which describes the logarithm of fitness as a negative linear function of the cumulative inbreeding coefficient:

$$\ln W = -A - BF \quad \text{or} \quad W = \exp(-A - BF), \quad (2)$$

where  $W$  is fitness,  $A$  is the reduction in fitness caused by environmental and genetic effects that are independent of inbreeding, and  $F$  is the inbreeding coefficient. The coefficient  $B$  measures the rate at which survival decreases with increased inbreeding; it is commonly viewed as the number of "lethal equivalents" per gamete and includes the effects of independently acting lethal alleles as well as the cumulative effects of partially deleterious alleles that would kill the individual if made homozygous. The model was originally designed for survival, but it can easily be extended to fecundity (Charlesworth and Charlesworth 1987).

This log-linear formulation assumes independence between genetic and environmental causes of reduced fitness and that genetic effects are multiplicative across loci. The model specifically assumes an absence of nonlinear effects that might arise from synergistic fitness interactions among genetic loci. There is considerable empirical support, however, for synergism in *Drosophila* (Kosuda 1972; Simmons and Crow 1977) and Japanese quail (*Coturnix coturnix japonica*; Sittmann et al. 1966), yielding nonlinear results for higher values of  $F$ . If the relationship between inbreeding and fitness is synergistic across loci, we can replace equation (2) with a polynomial in  $F$ :

$$\ln W = -A - BF - CF^2 - DF^3 \dots, \quad (3a)$$

where the intercept  $A$  still represents inbreeding-independent fitness reduction. Synergism can take almost any conceivable form, and the polynomial is best viewed as a Taylor expansion version of a more complicated (but unknown) function of  $F$ . Empirical data (Sittmann et al. 1966; Kosuda 1972; Simmons and Crow 1977) suggest a concave downward function for fitness. No great weight can be attached to the precise coefficients, and, as a matter of sheer mathematical convenience, we assume that  $B = C = D = \dots = \beta$ , which is probably generous to the higher-order terms. That reduces equation (3a) to the form

$$\ln W = -\alpha - \beta(F + F^2 + F^3 \dots), \quad (3b)$$

where  $\alpha = A$ . Now,  $0 < F < 1$ , so

$$F + F^2 + F^3 \dots = F/(1 - F) = G, \quad (4)$$

so we can replace equation (3b) with

$$\ln W = -\alpha - \beta G \quad \text{or} \quad W = \exp(-\alpha - \beta G). \quad (5)$$

In general,  $\beta < B$  (see Mills [1993, chap. 1] for further comparison of synergistic and linear models).

### *Inbreeding Depression and Demographic Rates*

We incorporate inbreeding depression directly into the vital rates of the Leslie matrix, using a strategy similar to that used previously for density dependence (Smouse and Weiss 1975; Weiss and Smouse 1976). In the absence of inbreeding ( $F = 0$ ), the survival probability for the  $i$ th cohort is

$$P_i(F = 0) = P_i = \exp(-\alpha_i), \quad (6)$$

the standard Leslie (1948) result. In the presence of inbreeding ( $F > 0$ ), the value is

$$P_i(F > 0) = \exp(-\alpha_i - \beta_i G(t - i)) = P_i \exp(-\beta_i G(t - i)). \quad (7)$$

We use  $G(t - i)$  because individuals in the  $i$ th age class at time  $t$  were born in time interval  $(t - i)$  and so have the inbreeding coefficient for that cohort (recall that  $G = F/(1 - F)$ ).

By a similar line of reasoning, the inbred fecundity of the  $i$ th cohort is

$$M_i(F > 0) = M_i \exp(-\delta_i G(t - i)), \quad (8)$$

where  $\delta_i$  represents the impact of inbreeding on fecundity. Clearly, the inbred "fertility" of the  $i$ th cohort must be

$$P_0(F > 0)M_i(F > 0) = P_0M_i \exp(-(\beta_0 + \delta_i)G(t - i)). \quad (9)$$

We replace the constant Leslie projection matrix  $X$  with  $X(G, t)$ , which depends on the inbreeding history of the population, with  $P_i$  replaced by  $P_i(G(t))$  and  $M_i$  replaced by  $M_i(G(t))$ . That converts the recurrence relation to

$$N(t + 1) = X(G, t)N(t). \quad (10)$$

Other demographic variables can be modified in a similar fashion to account for inbreeding depression. For example, the probability ( $L_i$ ) of surviving from birth to the beginning of age class  $i$  (the survival rate function) takes the form

$$L_i(G(t)) = P_0P_1 \cdots P_{i-1} \cdot \exp\left(-\sum_{j=0}^{i-1} \beta_j G(t - j)\right). \quad (11)$$

As an expression of the inbreeding coefficient, the  $G$  value is itself a changing function of the population's demographic characteristics. At time  $t = 0$ , we assume that the population is isolated but males and females are not yet inbred ( $F(0) = G(0) = 0$  for all cohorts). Real populations often would begin with a set of nonzero values, but because we are interested in incremental values of inbreeding we take the traditional approach of beginning with  $F(0) = 0$ . Infants born during time interval  $t$  have inbreeding coefficient  $F_0(t)$ , based on the effective population size,  $N_e(t)$ , and on the average accumulated inbreeding coefficient,  $\hat{F}(t)$ , carried by parents contributing to the new cohort at time  $t$ :

$$F_0(t) = 1 - \{[1 - \bar{F}(t)] \cdot [1 - (1/2N_e(t))]\}. \quad (12)$$

The quantity  $\bar{F}(t)$  is a weighted average of the  $F$  values for the previous  $K$  time periods (cohorts):

$$\bar{F}(t) = \frac{N_1(t)M_1(t)F(t-1) + \cdots + N_K(t)M_K(t)F(t-K)}{N_1(t)M_1(t) + \cdots + N_K(t)M_K(t)}. \quad (13)$$

Effective population size depends directly on population size and the costs of inbreeding on demographic vital rates. For females, we calculate  $N_e$  for each time interval ( $N_{ef}(t)$ ) by a formula that accounts for overlapping generations (Lande and Barrowclough 1987):

$$N_{ef}(t) = \{[N_f(t) \cdot R_0(t)] - 1\} / \{R_0(t) + [V_f(t)/R_0(t)] - 1\}, \quad (14)$$

where  $N_f(t)$  is the census number of females, and  $R_0(t)$  is the net reproductive rate, the average number of female progeny produced by a female during her lifetime:

$$R_0(t) = L_1(t)M_1(t) + \cdots + L_K(t)M_K(t). \quad (15)$$

The variance of lifetime progeny number among females,  $V_f(t)$ , is a function of both variation in time of death and variation in reproductive output among females of any particular age class (see App. A):

$$V(t) = R_0(t) + \sum_{k=0}^K (L_k(t) - L_{k+1}(t))(\bar{M}_k - R_0(t))^2. \quad (16)$$

To convert the single-sex (female-dominant) demographic treatment into a two-sex model for mammals, we invoke a two-sex  $N_e$  formulation (see Crow and Kimura 1970):

$$N_e(t) = \frac{4N_{em}(t)N_{ef}(t)}{N_{em}(t) + N_{ef}(t)}, \quad (17)$$

where  $N_{em}(t)$  and  $N_{ef}(t)$  are the effective population sizes for males and females, respectively, at time  $t$ . Using  $\theta$  to represent the effective sex ratio, and  $N_{ef}(t)$  as described in equation (14), we define

$$N_{em}(t) = \theta * N_{ef}(t), \quad (18)$$

permitting conversion of  $N_{ef}(t)$  into a two-sex analogue:

$$N_e(t) = \left( \frac{4\theta}{1 + \theta} \right) N_{ef}(t). \quad (19)$$

As a reasonable first approximation, the relationship between  $N_{em}(t)$  and  $N_{ef}(t)$  is determined more by mating system than it is by shifting demographic detail, so we treat  $\theta$  as an adjustable parametric constant of the model.

#### STOCHASTIC POPULATION GROWTH OR EXTINCTION

Given the current population size vector,  $\mathbf{N}(t)$ , and the corresponding projection matrix,  $\mathbf{X}(G(t))$ , we next impose stochastic variation, including both "envi-

ronmental" and "demographic" randomness. We model environmental variation by introducing random changes in the averages of all demographic rates. As a first cut from the wide range of possible variance in demographic rates, we chose a coefficient of variation of 0.3 on the basis of both the literature from which we obtained our mean vital rates (see below) and on studies examining mammal populations over time (e.g., Myers et al. 1985; Dobson and Murie 1987).

The correlation between demographic rates is an important factor of population persistence (Doak et al., in press), but no general rules govern such correlation. We take the simple approach that environmental fluctuations affect survival and fecundity in the same direction but not necessarily to the same degree, assuming further that all age classes are affected equally. Survival is bounded by zero and one, so we sample survival from a beta distribution (Doak 1989; Doak et al., in press) with the mean and variance for that age class. To sample fecundity, we first choose a random normal deviate, with a mean of zero and the age-specific variance. Whether the absolute value of the deviate is added to or subtracted from mean fecundity depends on whether survival is above or below the mean for that time step. (Fecundity cannot be negative.) This process repeats for each time step, using vital rates at time  $t$ , as modified by the inbreeding coefficient (and hence  $G(t)$ ) of each cohort.

We use these environmentally randomized vital rates as the parametric mean  $P_i(t)$  and  $M_i(t)$  for Monte Carlo sampling of demographic stochasticity. For each individual in the  $i$ th age class, we draw a random number,  $u$ , from the uniform distribution  $U(0, 1)$ . If  $u \leq P_i(t)$ , the individual survives into the next age class. The number of offspring for each individual is drawn from a Poisson distribution with mean  $M_i(t)$ . For each offspring, we draw a uniform random number,  $v \in U(0, 1)$ ; if  $v \leq P_0(t)$ , the newborn survives into the first age class.

### *Simulated Vertebrate Populations*

For small populations with negative intrinsic growth rates ( $\lambda < 1$ ), inbreeding is not the critical issue, although it can certainly exacerbate the situation. Our concern here is an organism with a positive growth rate ( $\lambda > 1$ ), whose habitat has been fragmented into isolated patches that are small enough to place the resident populations in danger of stochastic extinction.

To maximize generality, we model a range of intrinsic growth rates, inbreeding costs, initial population sizes, and breeding sex ratios. We use three life histories, each composed of 10 age classes (table 1), to encompass the range of growth rates expected for nondeclining mammals. The demographic schedule with the lowest growth rate ( $\lambda = 1.05$ ) is typical of an ungulate (see, e.g., McCullough 1979; Clutton-Brock et al. 1987). Next, we use a demographic schedule with a "medium" growth rate ( $\lambda = 1.24$ ), characteristic of a medium-sized felid (Eisenberg 1981; Beier 1993). Finally, we examine a "high" growth rate ( $\lambda = 1.56$ ), arising from a life table resembling that for a microtine rodent (French et al. 1975; Hansson and Henttonen 1985). Low but positive growth rates are usual for wild mammals, but a value as large as  $\lambda = 1.56$  is seldom attained by wild mammal populations (Pianka 1970; Robinson and Redford 1986), and we can view it as an almost unattainable upper limit.

We also assess a range of inbreeding costs ( $\beta$  and  $\delta$ ) from zero to near the

TABLE 1  
 STYLIZED INBREEDING-INDEPENDENT VITAL RATE SCHEDULES USED IN SIMULATIONS

AGE CLASS	UNGULATES		FELIDS		RODENTS	
	$P_i$	$M_i$	$P_i$	$M_i$	$P_i$	$M_i$
0	.65	.00	.60	.00	.75	.00
1	.90	.00	.75	.00	.80	.00
2	.95	.15	.80	1.00	.85	1.00
3	.95	.40	.80	1.20	.90	2.00
4	.95	.50	.85	1.50	.90	2.50
5	.95	.50	.85	1.50	.95	3.00
6	.95	.50	.80	1.50	.95	3.00
7	.80	.30	.70	1.50	.85	2.50
8	.40	.15	.60	1.00	.70	1.50
9	.20	.05	.30	.00	.40	.50
10	.00	.00	.00	.00	.00	.00
Growth rate ( $\lambda$ )		1.05		1.24		1.56
$R_0$		1.26		2.36		6.84
Generation interval ( $T$ )		4.79		4.37		5.00

NOTE.—Age classes (and time intervals) can be viewed as 1 yr for ungulates and felids and 3 wk for rodents. We assume prebreeding censusing, so  $P_0$  is the probability of a newborn infant surviving to its first census, and  $M_0$  and  $P_{10}$  are set equal to 0 by convention.

maximum found in the published literature. Several studies quantify inbreeding costs for natural insect and plant populations (reviews in Mitton and Grant 1984; Charlesworth and Charlesworth 1987), but similar data for normally outbred vertebrates are limited. We use what information there is to establish reasonable bounds for our inbreeding depression parameters, namely  $0 \leq \beta, \delta \leq 1.0$  (App. B). Our model can incorporate age-specific inbreeding costs, but we limit exploration here to single  $\beta$ 's and  $\delta$ 's, applied uniformly across age classes.

We also consider different initial population sizes:  $N(0) = 5, 20,$  and  $80$ . We randomly assign individuals to cohorts at the beginning of each simulation, with the probability of being in any age class being the Leslie stable age-distribution proportion. We encompass the mating system and other nongenetic factors affecting sex ratio by setting  $\theta$  in equation (19). The life histories we model are intended to be general, so we use a range of  $\theta$  from 0.1 to 1.0 with each of the three life histories.

For each set of parameter inputs, we simulate 500 replicate populations for 20 time steps, which is less than five generations for all three life histories (table 1). Results are unaffected by the real-time interval represented by a single step, but for the sake of reality one can assume a time step equal to a birth pulse of 1 yr for the "ungulate" ( $\lambda = 1.05$ ) and "felid" ( $\lambda = 1.24$ ) populations and 3 wk for the "rodent" ( $\lambda = 1.56$ ) population.

#### *Population Extinction without Inbreeding Depression*

The theory of stochastic birth and death processes in models without age structure stresses the importance of variance in growth rate, as affected by environmental stochasticity, in determining the time to extinction (see, e.g., Leigh 1981; Goodman 1987). For a given level of environmental variance, the probability of

TABLE 2

POPULATION GROWTH WITHOUT INBREEDING: MEAN (AND SE) OF FEMALE POPULATION SIZE, AND PERCENTAGE OF 500 STOCHASTIC SIMULATIONS THAT WENT EXTINCT BY VARIOUS TIME INTERVALS

TIME STEP	UNGULATES ( $\lambda = 1.05$ )		FELIDS ( $\lambda = 1.24$ )		RODENTS ( $\lambda = 1.56$ )	
	Mean $N$ (SE)	% Extinct	Mean $N$ (SE)	% Extinct	Mean $N$ (SE)	% Extinct
$N(0) = 5$ :						
5	6.7 (.2)	17.6	14.9 (.7)	7.6	52.5 (2.2)	5.6
10	9.2 (.5)	30.0	49.9 (4.0)	15.2	555.0 (34.1)	7.0
15	11.8 (1.0)	41.2	136.2 (12.7)	17.4	5,525.0 (440.7)	7.6
20	16.5 (1.6)	49.4	485.0 (77.5)	20.6	54,503.6 (6,434.6)	8.0
$N(0) = 20$ :						
5	26.9 (0.7)	8.8	62.2 (2.6)	1.2	205.5 (7.3)	1.0
10	36.3 (1.6)	17.2	193.9 (12.1)	3.4	2,053.9 (106.7)	2.4
15	52.4 (3.1)	24.0	615.0 (53.8)	4.6	19,292.5 (1,387.2)	2.4
20	68.0 (4.7)	31.2	1,669.9 (202.2)	6.4	176,599.0 (15,517.4)	2.4
$N(0) = 80$ :						
5	108.1 (2.8)	2.0	262.6 (9.9)	0	...	...
10	141.0 (5.7)	6.8	810.1 (52.3)	0.2	...	...
15	195.8 (10.9)	12.2	2,496.9 (214.3)	0.6	...	...
20	279.6 (18.9)	17.4	7,636.1 (937.4)	0.8	...	...

NOTE.—Starting conditions are based on three different sets of generalized life histories and three different initial numbers of females. Time steps can be thought of as 1 yr for the ungulate and felid populations, and 3 wk for the rodent population.

\* Simulating such numbers with our model is prohibitive; obviously, very few of these populations go extinct.

extinction decreases, to varying extents, as the intrinsic growth rate and/or the population ceiling increases (Lande 1993). We find similar results for our age-structured model without a population ceiling: extinction probability within 20 time steps decreases as  $\lambda$  and initial population size increases (table 2). Without inbreeding depression or density dependence, rodent populations grow too fast to be very vulnerable to stochastic extinction. The felid populations are vulnerable for small  $N(0)$  but much less so for larger  $N(0)$ . Ungulate populations remain vulnerable to stochastic extinction for all three initial population sizes (table 2).

In the absence of inbreeding depression, and with a sex ratio of unity ( $\theta = 1.0$ ), the ( $N_e/N$ ) ratio is approximately 0.3–0.5, compatible with the upper range of measured values for a variety of wild mammals (Ryman et al. 1981; Chepko-Sade and Halpin 1987; Smith and McDougal 1991). Both inbreeding depression and a skewed sex ratio lowered the  $N_e/N$  ratio.

#### *Inbreeding Effects Are Mediated by Population Size and Growth Rate*

Inbreeding depression can lower the survival rate of small, stochastically fluctuating populations, as the buildup of inbreeding progressively decreases  $R_0(t)$  and  $\lambda$ . As anticipated, inbreeding builds up faster in populations that are initially small. For example, consider population trajectories for the intermediate (felid) demographic schedule, using a modest level of inbreeding depression ( $\beta = \delta = 0.5$ ). A small starting number of females ( $N(0) = 5$ ) leads to extinction of all 500



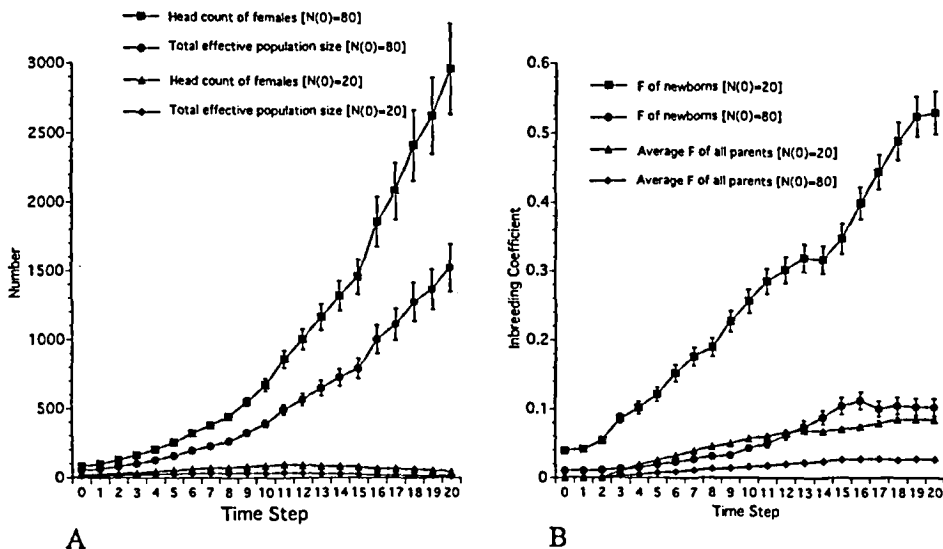


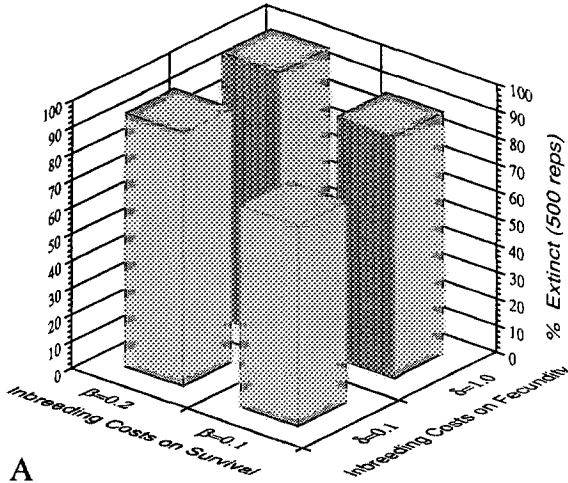
FIG. 1.—Projection for 20 time steps of intermediate (felid,  $\lambda = 1.24$ ) demography, with equal sex ratio ( $\theta = 1.0$ ) and a medium level of inbreeding depression imposed ( $\beta = \delta = 0.5$ ). Two initial female population sizes ( $N(0) = 20$  and  $N(0) = 80$ ) are shown. A, Mean (and SE) of trajectories for female population size  $N(t)$  and overall effective population size  $N_e(t)$ ; B, mean (and SE) of trajectories for inbreeding coefficient of newborns  $F_0(t)$ , and the average inbreeding coefficient of parents  $\bar{F}(t)$ .

replicates by time step 15; the  $F$  of newborns accumulates rapidly, and  $N(t)$  and  $N_e(t)$  quickly decline (Mills 1993). In larger populations, where  $N(0) = 20$  and 80, both  $N(t)$  and  $N_e(t)$  grow more rapidly, with inbreeding accumulating more slowly (fig. 1).

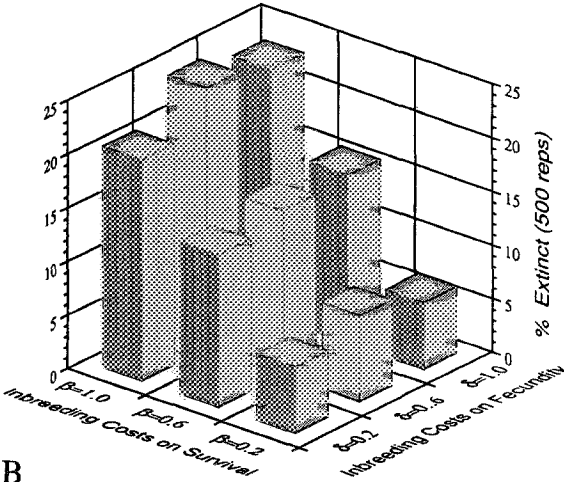
With respect to extinction probability, we again see the effect of starting population size and growth rate on the rate of inbreeding accumulation. Figure 2A shows extinction probabilities for the intermediate demographic schedule, with variable levels of inbreeding depression ( $0.0 \leq \beta, \delta \leq 1.0$ ),  $\theta = 1$ , and  $N(0) = 5$ ; the corresponding results for  $N(0) = 80$  are shown in figure 2B. In both cases, even minor inbreeding depression boosts extinction probability above that expected in the absence of inbreeding ( $\beta = \delta = 0$ ; table 1).

The only escape from inadequate initial numbers is for the population to grow to large size before inbreeding depression effects can accumulate. The role of intrinsic growth rate emerges from a comparison of the three demographic schedules, all with  $\theta = 1.0$  and a small initial population size ( $N(0) = 5$ ). Most rodent populations persist unless inbreeding costs are quite high (fig. 3A), whereas the ungulate populations (fig. 3B) suffer nearly certain extinction for even tiny costs. Felids (fig. 2A) exhibit intermediate behavior.

In all cases, survival depression ( $\beta$ ) has a bigger impact than comparable fecundity depression ( $\delta$ ). Leslie (1948, 1959) and previous studies (Smouse and Weiss



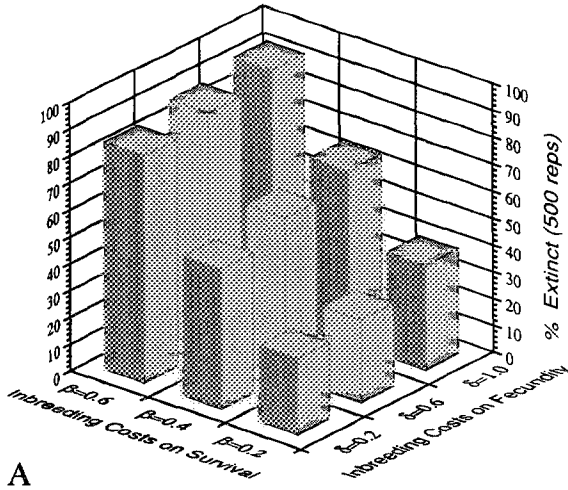
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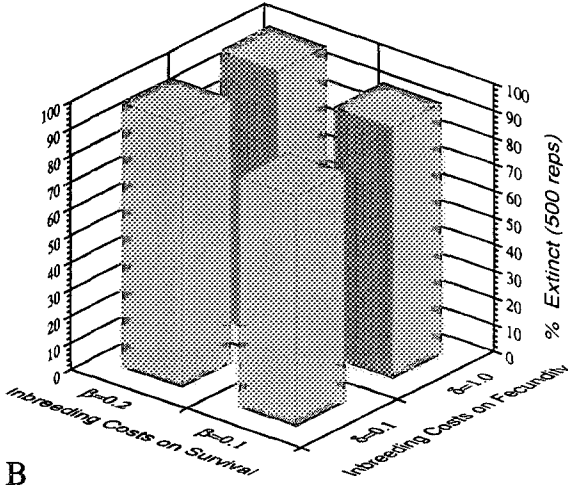
B

FIG. 2.—The effects of variable survival ( $\beta$ ) and fecundity ( $\delta$ ) depression on the probability of extinction, for intermediate ( $\lambda = 1.24$ ) demography and sex ratio set at  $\theta = 1$ , (A) with initial population set at  $N(0) = 5$  and (B) with initial population set at  $N(0) = 80$ .

1975; Weiss and Smouse 1976) all showed a similar trend for density-dependent damping in Leslie models. One reason for this is that depression of  $P$  values (including  $P_0$ ) reduces  $R_0(t)$  more than does a depression of  $M$  values. A reduction in  $R_0(t)$  ultimately reduces  $N_e(t)$ , which further exacerbates the inbreeding depression, reducing  $R_0(t)$  still further. In addition, the inbreeding coefficient of newborns accumulates much faster than that of the long-lived parents (fig. 1A); the higher inbreeding coefficients for newborns means that the survival rates of these cohorts are more vulnerable to inbreeding depression than are the fecundities of their parents.



A



B

FIG. 3.—The effects of variable survival ( $\beta$ ) and fecundity ( $\delta$ ) depression on probability of extinction, for populations of varying growth rate with sex ratio set at  $\theta = 1$  and initial population set at  $N(0) = 5$ : A, high growth rate ( $\lambda = 1.56$ ); B, low growth rate ( $\lambda = 1.05$ ).

### *Inbreeding Effects Are Mediated by Sex Ratio*

In our simulations the sex ratio  $\theta$  is important only for its effect on  $N_e$ , and hence on  $F(t)$ ; in the absence of inbreeding depression ( $\beta = \delta = 0$ ), it does not affect the probability of extinction. If there is a cost to inbreeding, then  $\theta$  can have a major effect on extinction probability. The more polygynous the population, the lower will be  $N_e$ , the faster the buildup of inbreeding, and the greater the extinction probability for any initial population size and  $\lambda$  value. For example, we present the felid case in figure 4, with  $\delta = 0$  and  $N(0) = 20$ , but with  $\beta$  and  $\theta$  varying ( $0 \leq \beta, \theta \leq 1.0$ ). As before, the higher the value of  $\beta$ , the higher the

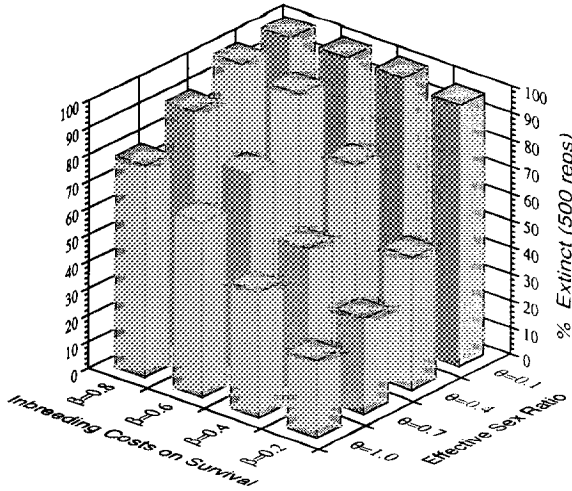


FIG. 4.—The effects of variable survival ( $\beta$ ) depression and sex ratio ( $\theta$ ) on the probability of extinction for medium growth ( $\lambda = 1.24$ ) demography, with fecundity depression set at  $\delta = 0$  and initial population set at  $N(0) = 20$ .

extinction probability. Furthermore, for any given value of  $\beta$ , lowering  $\theta$  raises the extinction probability. The same trends emerge from the other demographic schedules and starting population sizes.

#### DISCUSSION

Commendable attempts to broaden the scope of population viability analysis beyond an obsession with genetics (e.g., Dawson et al. 1987; Lande 1988; Dinerstein and McCracken 1990) have often been interpreted as posing a dichotomy between inbreeding depression and environmental and/or demographic fluctuations as causes of extinction. Our simulations show that this dichotomy is false. By demonstrating explicitly that both genetic stochasticity (i.e., inbreeding) and nongenetic stochastic forces are critically important to extinction probability, we hope to end the discussion of which factor is more important and focus attention on interactions between them.

#### *Purging of the Gene Pool*

The context of our simulations is that of a vertebrate population recently isolated by severe habitat alteration, an increasingly relevant scenario (see, e.g., Bierregaard et al. 1992; Mills 1993). Natural populations of vertebrates are generally outbred (reviews in Ralls et al. 1986; Templeton 1987), so that we expect the full costs of inbreeding to be realized. To the extent that a small starting population has already been "purged" of deleterious alleles by previous inbreeding, however, the incremental cost of additional inbreeding might be reduced (Chepko-Sade et al. 1987; Sjogren 1991; Ribble and Millar 1992). Whether or not

the incremental losses are smaller if we begin with partially inbred populations, we show that even small levels of inbreeding depression can enhance the extinction probability over that imposed by sheer environmental and demographic randomness.

Considerable controversy surrounds the extent to which inbreeding costs change over time in a population. Various works assert that the purging of the genetic load proceeds at a rate dependent on the accumulated inbreeding coefficient and the rate of previous inbreeding (e.g., Tantawy 1957a; Latter and Robertson 1962; Templeton 1987; Ehiobu et al. 1989; Barrett and Charlesworth 1991). There are conflicting or ambiguous reports of the same phenomenon (Tantawy and Reeve 1956; Tantawy 1957b), however, and in any case a purging of deleterious alleles over the long term leads to decreased population fitness over the short (five generations) term (Brewer et al. 1990; Barrett and Charlesworth 1991; Ribble and Millar 1992).

We take the position that an explicit incorporation of changes in inbreeding costs ( $\beta$  and  $\delta$ ) with changing rate of inbreeding ( $\Delta F$ ) would be complex and arbitrary, given the paucity of data from wild populations. Instead, we use a short projection interval of  $\leq 5$  generations and a curvilinear relationship between  $F$  and inbreeding costs to capture the essential pattern in a simple fashion. We follow Tantawy and Reeve (1956), who suggest that the disproportionately lower fitness under rapid inbreeding comes from the curvilinear decrease in fitness as  $F(t)$  increases, that is, from synergism (R. Frankham, personal communication). Also, in only five generations, high  $F(t)$  values can only be achieved by rapid inbreeding; populations under rapid inbreeding suffer disproportionate costs because they move quickly down the nonlinear curve. Thus, our  $G(t)$  encompasses the effects of synergism, as well as the short-term impact of nonlinearity that arises from purging.

#### *The Conservative Nature of Our Simulations*

There are several reasons to believe our results are conservative with respect to the impact of inbreeding depression on short-term population survival. First, we probably are not modeling the full range of inbreeding costs that are relevant in the wild. Most studies examining the costs of inbreeding have been conducted under relatively benign conditions in zoos or laboratories. If inbred individuals are less fit under stressful field conditions, then our "cost of inbreeding" values ( $\beta$  and  $\delta$ ) are underestimates (Hedrick and Miller 1992). On the other hand, costs of inbreeding could be overestimates if inbreeding depression in early life-cycle stages is compensated for in later stages (see, e.g., Van Noordwijk and Scharloo 1981).

Second, we did not impose negative density-dependent damping on the vital rates. With such damping, population growth is constrained even further (Smouse and Weiss 1975; Weiss and Smouse 1976), the inbreeding coefficient would accumulate faster, and fitness decrements could only be larger. The effect of positive density dependence, where survival and fecundity increase with density in small populations (Dennis 1989), is presumably in the opposite direction.

We assume that even our most vulnerable "organism" is capable of positive

population growth in the absence of inbreeding. The usual consequence of habitat fragmentation is a reduction in the ecologically determined growth rate, and the real problem—as often as not—is that  $\lambda < 1$ . In this situation, the first task is to elevate the rate of increase; otherwise, we will certainly lose the population, and inbreeding can only hasten the process. Our simulations indicate, however, that there is no justification for a generic claim that, if a population is small enough to be affected by inbreeding, then it will first become extinct because of stochastic fluctuations. The two phenomena go hand in hand. Qualitatively similar results have been discussed in the context of “mutational meltdown” for non-age-structured populations with deleterious mutations and density-dependent stochastic population regulation; mutation accumulation reduces population size, facilitating the overpowering of selection by genetic drift, which further increases the probability of fixing deleterious alleles (Lynch and Gabriel 1990; Gabriel et al. 1991).

### *Management Implications*

In addition to formalizing the relationship between inbreeding depression and the probability of stochastic extinction, the present effort yields several points of relevance to theory and management. First, our finding that extinction probability is more sensitive to survival depression ( $\beta$ ) than to fecundity depression ( $\delta$ ) implies that, all else being equal, researchers concerned with extinction probability for a particular species should give priority to quantifying inbreeding costs on survival. We hasten to add, however, that we still have no clear sense of which vital rates are most affected by inbreeding in mammals, and if it is true that litter size reduction is the most prominent effect of inbreeding in vertebrates (see Van Noordwijk and Scharloo 1981) then a primary focus on survival would be a mistake. We clearly need additional field studies on both components of inbreeding depression.

Second, we note the impact of sex ratio in affecting how inbreeding alters extinction probability. In general, there is little that can be done to increase  $\theta$  in natural populations, but it is important to consider that a skewed sex ratio can increase the probability of extinction. For example, Scribner et al. (1991) showed that a policy of “bucks only” hunting drastically unbalanced the reproductive sex ratio in favor of females, having profound consequences for  $N_e$  (see also Ryman et al. 1981).

Third, connecting genetic processes to the demography of isolated small populations is a critical part of building multiple-population models that include genetic considerations (Harrison 1991). Varvio et al. (1986) point out that managers concerned with several populations must compromise between maximizing variation within populations and maximizing total genetic diversity across populations, with the trade-off hinging on whether isolates can tolerate the homozygosity generated by small size. Our approach directly addresses this issue, which also has implications for the value of single large reserves relative to several small ones (Simberloff and Abele 1982).

We do not address here the implication of genetic exchange among small fragmented reserves. The overall  $N_e$  of a collection of semi-isolated fragments is

enhanced by genetic exchange, and extinction probability may be counterbalanced by recolonization potential (see, e.g., Gilpin and Hanski 1991). Moreover, the genetic variability of a local population can be enhanced with even small levels of gene flow (Levin 1988), reducing genetic load.

In closing, we reiterate that our results do not implicate inbreeding depression as the sole factor in the extinction of small, isolated populations. A high population growth rate can largely obviate the effects of short-term inbreeding depression, and population growth rates are fundamentally affected by habitat and/or environment quality. While extinction is a demographic process quite often dominated by factors that are extrinsic to the organism (Lande 1988), our work demonstrates that the potential impact of inbreeding depression can be important and sometimes pivotal.

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#### APPENDIX A

##### VARIANCE IN REPRODUCTIVE CONTRIBUTIONS

Consider a population at time 0. The average reproductive contribution of an individual is given by

$$R_0(t) = L_1(t)M_1(t) + \dots + L_k(t)M_k(t). \quad (A1)$$

This is a cross-sectional average for the different cohorts in the population, each of which has a slightly different inbreeding coefficient. We shall suppress the time-dependence ( $t$ ) notation here, but all the parameters depend on  $t$ , through  $F(t)$  and  $G(t)$ . The lifetime reproductive variance among females is measured relative to their average,  $R_0(t)$ , and it contains two components: (a) variance due to the fact that females cease reproduction and die at different ages and (b) reproductive variation among females of a given cohort.

Begin with a newborn. With probability  $(1 - P_0) = (L_0 - L_1)$ , the newborn does not survive into the first age class; this individual has zero reproductive contribution,  $M_0 = 0$ . We use the convention here that  $L_0 = 1$ . With probability  $P_0(1 - P_1) = (L_1 - L_2)$ , a newborn survives into age class 1 but not into age class 2. The average individual in this class has a reproductive contribution of  $M_1$ ; the class contribution is thus  $(L_1 - L_2)M_1$ . There is reproductive variation within the cohort during this time interval. We use a Poisson process to represent that reproductive variation within the first age class, so the variance is equal to the mean,  $M_1$ . With probability  $P_0P_1(1 - P_2) = (L_2 - L_3)$ , a newborn survives into age class 2 but not into age class 3. Such individuals experience two bouts of reproduction, and their average reproductive output is given by  $(L_2 - L_3)(M_1 + M_2)$ .

Among these individuals, there is also variation in reproductive output, both during the first age class and during the second. The variance for the first bout of reproduction is  $M_1$  and that during the second bout is  $M_2$ . We continue in this fashion until the last remnant of the cohort dies (after age class  $K$ ). If we tally the portion of the variance due to differential age at death, we obtain a variance among cohorts:

$$\sum_{k=0}^K (L_k - L_{k+1})(M_0 + \dots + M_k - R_0)^2 = \sum_{k=0}^K (L_k - L_{k+1})(\bar{M}_k - R_0)^2, \quad (A2)$$

where  $\bar{M}_k = \sum_{j=0}^k M_j$ . The within-cohort variance is

$$\begin{aligned} (L_0 - L_1) \cdot M_0 + (L_1 - L_2) \cdot (M_0 + M_1) + \dots + (L_K) \cdot (M_0 + \dots + M_K) \\ = (L_0 M_0 + L_1 M_1 + \dots + L_K M_K) = R_0. \end{aligned} \quad (A3)$$

The sum of these two components is thus (with the time subscript restored)

$$V(t) = R_0(t) + \sum_{k=0}^K (L_k(t) - L_{k+1}(t))(\bar{M}_k - R_0(t))^2. \quad (A4)$$

### APPENDIX B

#### ESTIMATING THE COST OF INBREEDING

Our method of determining  $\beta_i$  and  $\delta_i$ , under the assumption of inbreeding synergism, is similar to the calculation of lethal equivalents described in Morton et al. (1956; see also Charlesworth and Charlesworth 1987). The fundamental difference is in the substitution of  $G = F/(1 - F)$  for  $F$  itself. We extract estimates of  $\beta$  (and also  $\delta$ ) from the literature as follows.

Most literature deals with fitness as a decreasing log-linear function of  $F$ :

$$W(F) = \exp(-\hat{A} - \hat{B}F). \quad (B1)$$

Our synergistic inbreeding cost relationship substitutes  $W(G)$  for  $W(F)$ , and  $\hat{\alpha} = \hat{A}$ :

$$W(G) = \exp(-\hat{\alpha} - \hat{\beta}G). \quad (B2)$$

Based on estimates of  $\hat{B}$  and  $\hat{A}$  from a given study on log-linear inbreeding costs, we can solve for  $W(F)$  at  $F = 0.5$ . We then determine the inbreeding cost estimate ( $\hat{\beta}$ ) at that inbreeding coefficient; the fitness decrement with this  $\hat{\beta}$  will be less than the log-linear decrement when  $F < 0.5$ , and greater when  $F > 0.5$ , in a manner consistent with synergistic inbreeding costs (see text):

$$\hat{\beta} = \left( \frac{-\ln W(G) - \hat{\alpha}}{\frac{F}{1 - F}} \right). \quad (B3)$$

If the published report does not include an estimate of  $A$ , the same equation is manipulated to yield an alternative estimate

$$\hat{\beta} = (\ln W(F = 0) - \ln W(F > 0)) \cdot \left( \frac{1 - F}{F} \right). \quad (B4)$$

The most comprehensive estimates for inbreeding depression on juvenile survival are those of Ralls et al. (1988), who found a median  $B$  of 1.6 and an upper quartile of 2.8 for 40 mammal species. Converted to  $\beta$  at  $F = 0.5$ , these data yield an estimated median of 0.8 and an estimated upper quartile of 1.4. Estimates of inbreeding costs for postjuvenile



survival are not as comprehensive, but a range extending to  $\beta = 1.0$  is reasonable for humans (Morton et al. 1956; May 1979) and wolves (Laikre and Ryman 1991). For fecundity, an extensive study of wild *Peromyscus* (Brewer et al. 1990; see also Keane 1990) indicates that synergistic inbreeding costs approach  $\delta = 1.0$  (see also Morton et al. 1956; Bowman and Falconer 1960; Sittmann et al. 1966; Van Noorwijk and Scharloo 1981).

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