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Genetically Effective Population Size of Large Mammals: An Assessment of Estimators

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Abstract: We calculated genetically effective population sizes (N_e) for simulated grizzly bear (*Ursus arctos*) populations by tracing the loss of heterozygosity through time, and compared them with estimates of N_e produced by applying published formulas to demographic results from the simulation. Estimates of N_e using different formulas on identical data varied widely. Equations published by Hill (1972), and modifications of those used by Ryman et al. (1981) and Reed et al. (1986), provided the most accurate estimates. Minor population fluctuations had little effect on N_e , but variation in lifetime reproductive success among males (V_{km}) greatly reduced N_e from its expectation under random mating success. All methods to estimate N_e for populations with complex demographics require extensive data, but estimates for V_{km} in polygynous species are especially difficult to obtain. We suggest that simulation modeling may provide alternative methods to estimate V_{km} and N_e .

Introduction

A growing concern in management of endangered species is the increasing insularity of small populations. Es-

Resumen: Calculamos tamaños de poblaciones genéticamente efectivas (N_e) para poblaciones simuladas del oso gris (*Ursus arctos*) trazando la pérdida de heterocigalidad a través del tiempo, luego las comparamos con estimaciones de N_e producidas aplicando fórmulas publicadas a los resultados demográficos de la simulación. Los valores de N_e calculados usando diferentes fórmulas con datos idénticos, variaron mucho. Las ecuaciones publicadas por Hill (1972), y modificaciones de las usuadas por Ryman, et al. (1981) y Reed et al. (1986), proporcionaron los cálculos más precisos. Fluctuaciones menores en las poblacionales tuvieron poco efecto sobre N_e , pero la variación en el éxito reproductivo por vida entre los machos V_{km} redujo tremendamente el N_e comparado con el valor esperado bajo éxito reproductivo al azar. Todos los métodos para calcular N_e para poblaciones con demografías complejas requieren datos extensos, pero estimaciones para V_{km} en especies polígamas son especialmente difíciles de obtener. Sugerimos que modelos de simulación pueden proveer métodos alternativos para calcular V_{km} y N_e .

pecially worrisome is the deterioration in genetic variation of many species of large mammals, where population densities are normally low and spatial requirements high, such as tigers (*Panthera tigris*) and rhinos (Rhinocerotidae). The most useful concept in estimating the magnitude of genetic loss through time to be expected in small, isolated populations is that of effective population size (Wright 1969). While there is

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universal agreement about the importance of estimating effective population size (N_e) for making informed management decisions (Soulé 1980), considerable confusion remains about exactly how it is best estimated, especially in the case of large mammals with their typically complex demographics and numerous departures from the genetically "ideal" population. The usual approach is to infer the rate of loss of genetic variation from the breeding structure of the population using various demographic statistics.

Wood (1987) described N_e as "something of a 'black box,' obscuring rather than illuminating the interactions and effects" of characteristics relevant to rate of loss of genetic diversity. Recently, numerous articles have attempted to provide guidance to managers of wild populations interested in estimating N_e (Ryman et al. 1981; Lemkuhl 1984; LaCava & Hughes 1984; Reed et al. 1986; Wood 1987; Lande & Barrowclough 1987; Crow & Denniston 1988). Unfortunately, they do not all use the same formulas, and applying their techniques results in differing estimates of N_e , and therefore of the rate of genetic loss to be expected over time.

Wright (1969) defined effective population number as "whatever must be substituted for N [population size] in the basic formula" (p. 211) whenever a population fails to meet genetically ideal conditions. Wright's "basic formula" defines the rate of loss of selectively neutral genetic variation (i.e., heterozygosity, H) as

$$H_t = H_0 [1 - 1/(2N)]^t \quad (1)$$

where t is time in generations.

Estimates of N_e for populations of large mammals have addressed one or more of the following characteristics of non-ideal populations:

- (1) unequal number of breeding males and females (the ideal population assumes monoecious individuals),
- (2) fluctuations in population size,
- (3) overlapping generations,
- (4) non-Poisson (and nonbinomial) variance in distribution of offspring surviving to adulthood (the ideal population assumes all individuals have equal probability of contributing to subsequent generations),
- (5) heritability of fertility (the ideal population assumes none), and
- (6) geographic structure (the ideal population assumes random mating, i.e., panmixia).

In this paper, we compare approximations of N_e calculated from published demographic formulas to known N_e values from simulated grizzly bear populations. We focus particularly on those formulas that claim to be applicable to populations of large mammals. Thus, for example, we do not examine papers dealing with pop-

ulations of a single sex, or those having discrete generations. Grizzly bears have many attributes (e.g., polygyny, delayed reproduction, extended parental care, between-sex differences in breeding success and survival of offspring) that make them an appropriate choice for assessing the application of published N_e formulas to other large mammals. We conclude with a discussion of the difficulties in obtaining data necessary to apply published N_e formulas to wild populations. We suggest that simulations may provide a method to estimate parameters that are otherwise difficult to gather in the field.

Model

The simulation model was a discrete-time, stochastic computer program that followed the history of each individual bear from birth until death.* The model retained information on each bear's age, sex, parents, mates, offspring, membership in a family group, and, if female, whether attended by offspring, pregnant, or solitary, thus allowing calculation of various demographic statistics required by N_e formulas. Five events affected each bear during the simulation year: breeding, hunting mortality, natural mortality, birth, and family breakup (weaning of juveniles). At each event, an individual bear's fate (dying, giving birth, etc.) was determined by comparing its age-specific probability with a random number from a uniform (0,1) probability distribution.

We limited our investigations to stable, stationary populations (i.e., those populations with similar numbers and age structures from year to year). To achieve equilibrium conditions in both hunted and unhunted populations, survival and natality were modeled as density-dependent functions of population size (N) relative to a hypothetical carrying capacity (K). Survival and natality rates increased slightly above mean values when a population fell below $N/K = 1.0$; rates decreased slightly when a population increased above K .

We used 30 age classes, and natality and survival rates typical of Rocky Mountain populations of grizzly bears (Appendix A). To assess published formulas for estimation of N_e it is not necessary that our simulation model emulate wild grizzly bear populations accurately (although elsewhere we make the claim that our model structure and parameters were reasonable approximations; Allendorf et al., in preparation). It is only necessary that the model provide detailed demographic data with which to compare N_e estimates using the published formulas.

A critical component for estimating effective popula-

* *Generalized Animal Population Projection System (GAPPS)* is available for use on IBM-compatible microcomputers. For information about acquisition, contact the Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812.

tion size, for which data are lacking, is the distribution of reproductive contribution among males. We simulated three different male mating systems (Table 1) with the intent of embracing the range of probable values: (1) a "random" male mating system, in which adult males were picked at random (with replacement) to sire the offspring of each pregnant female, (2) our "best estimate" of the likely situation in a wild grizzly bear population, in which adult males of a subjectively selected prime age group (ages 8–18) were assumed to have dominant status and given higher probabilities of fathering cubs than were males of other adult ages, and (3) an "extreme" age-selective system, similar to (2), but with heavier weighting toward the prime age group. In all three systems, males less than four years old were considered subadults and did not sire cubs. None of the three male mating systems allowed for variability of breeding success within age classes. Thus, variation within a particular cohort was Poisson. In nature, individuals of the same age class might be expected to display heterogeneity in reproductive success over and above Poisson variance (i.e., dominant males).

We simulated three alternative hunting strategies (*sensu* Ryman et al. 1981) that we termed "random," "chance," and "trophy" (Table 2). Each differed in its assumptions about interactions between hunters and bears and hence in the age and sex of bears killed. In each case, we limited the harvest to 4% of the standing population each year to prevent populations from declining due to overharvest (Harris 1986). Under the "random" hunting strategy, bears were killed by hunters in proportion to their abundance in the population. Under the "chance" hunting strategy, bears were killed in proportion to their likelihood of being encountered by a hunter, which was assumed to be related to the bears' amount of movement (Bunnell & Tait 1980). Subadult males, assumed to wander about in exploratory forays, were the most vulnerable to harvest. Mothers with young, assumed to constrain their movements to relatively small areas, were the least vulnerable. Under "trophy" hunting, bears were killed in proportion to their size and assumed desirability as a trophy. Adult males, the largest bears, were the most vulnerable; adult females and subadult males less vulnerable. Hunters employing this strategy were assumed to frequently pass up

Table 1. Coefficients given to males of different ages in the simulation model governing their probability (relative to each other) of siring the cubs of a pregnant female. The model builds a cumulative distribution, so that the sum of all males' probabilities = 1.0.

Mating system	Age			
	0–3	4–7	8–18	19+
Random	0.00	1.00	1.00	1.00
Estimated	0.00	0.25	1.00	0.33
Extreme	0.00	0.03	1.00	0.04

Table 2. Coefficients given to animals of each sex-age class governing their vulnerability (relative to each other) of being hunted, according to 3 different hunting regimes: random, chance, and trophy. The model builds a cumulative distribution, so that the sum of all individuals' vulnerabilities = 1.0. Animals are picked at random (with replacement) for removal by hunting, and the process continues until the specified number are removed.

Category	Relative vulnerability					
	Random		Chance		Trophy	
	F	M	F	M	F	M
Age 0 with mother	1.00	1.00	0.05	0.05	0.00	0.00
Age 0 without mother	1.00	1.00	2.00	2.00	0.00	0.00
Cub >0 with mother	1.00	1.00	0.20	0.20	0.00	0.00
Mother with young	1.00	—	0.20	—	0.00	—
Age 1–3	1.00	1.00	2.00	7.00	0.00	0.00
Age 4	1.00	1.00	2.00	7.00	0.25	0.25
Age 5–7	1.00	1.00	0.80	1.00	0.25	0.25
Age 8–30	1.00	1.00	0.80	1.00	0.25	8.00

the opportunity to kill the more numerous younger (and smaller) bears, and avoid killing young or their attending mother in all cases.

Because our simulated grizzly bear populations exhibited relatively modest fluctuations, we also ran one set of simulations in which we deliberately inflated variances of vital rates to produce greater variation in population size.

Our simulation model did not include heritability of fertility, so we were unable to examine possible effects of this factor on the various estimators. With the exception of age-related mating probabilities for males as described above, the simulation also assumed complete panmixia.

Heterozygosity and N_e

We determined heterozygosity by calculating the inbreeding coefficient of individuals by the algorithm of Boyce (1983). This inbreeding coefficient (pedigree F ; Wright 1969, p. 177) is equal to the probability that two genes at a locus in an individual are identical by descent from an allele in the foundation population. Thus, F is an exact measure of the loss in heterozygosity, $H = (1 - F)$, over the entire genome relative to the founding populations (Wright 1969). The populations used to begin the simulations had age structures typical of grizzly bear populations; the initial heterozygosity (H_0) was taken to be 1.0 ($F = 0$) and all individuals were assumed to be unrelated.

We estimated the rate of loss of heterozygosity by regressing the natural logarithm of mean heterozygosity in newborns over time. From the basic formula (1),

$$H_t = H_0 [1 - (1/2N_e)]^t \quad (2)$$

but because $H_0 = 1$,

$$H_t = [1 - (1/2N_e)]^t \quad (3)$$

or,

$$N_e = 1/(-2 e^m + 2) \quad (4)$$

where t is the number of generations, and m is the slope of the natural log of mean heterozygosity of the newborn cohort regressed on time, measured in generations:

$$m = \frac{1}{H_t} \frac{dH_t}{dt} = \frac{d \ln(H_t)}{dt}$$

The generation interval is the mean age of parents contributing progeny, weighted by their number of progeny.

We note here that our procedure yields the *inbreeding* effective size (N_{ei}). Some of the demographic formulas we examined were clearly intended to yield this number, while others estimated the *variance* effective size (N_{ev}), and still others made no distinction between the two. In populations that are stable and stationary, as were our simulated populations, estimates of N_{ei} and N_{ev} converge (see Crow & Kimura 1970, p. 361; Wright 1969; Felsenstein 1971); thus no further distinction is made throughout this paper.

We performed 50 replicates for each combination of parameter values. Each replicate lasted 100 years; the first 24 years were omitted from the regression analysis to provide a delay of 2–3 generations in which the rate of increase in inbreeding reached an asymptote (Hill 1972, 1979; Johnson 1977). The mean inbreeding coefficient of newborns was calculated every five years, rather than each year, to save computing time. (We used population sizes of approximately 100, so that by the end of 100 years there were over 1,000 bears in each pedigree).

Demographic Estimation of N_e

We estimated N_e with demographic formulas by recording the relevant parameters during a simulation run of 76 years (years 25–100). Details of each demographic formula are presented in Appendix B. Estimators of N_e examined were:

- (1) Hill (1972), who presented a general formula (Eq. B1) for calculating N_e for populations of constant size and sex ratio with overlapping generations.
- (2) Ryman et al. (1981), who used formulas from Crow & Morton (1955) to calculate N_e (Eq. B2) from the demographic structure of the female component of simulated moose (*Alces alces*) populations in order to estimate effects of hunting on N_e .
- (3) An alternative estimator using the same structure as Ryman et al. (1981), but utilizing data for both

sexes, and calculating variances of offspring production directly from the simulated data rather than using the methods of Crow & Morton.

- (4) Lemkuhl (1984), who suggested a process to estimate the census number of breeding animals needed to achieve $N_e = 50$ (Soulé 1980), and thereby an estimator of N_e from N (Eq. B8).
- (5) LaCava & Hughes (1984), who asserted that the equation accounting for departures in equal sex ratio (Wright 1931; Crow & Kimura 1970) was sufficient to estimate N_e for polygynous species (Eq. B9).
- (6) Reed et al. (1986), who modified Hill's (1972) formula for the case in which reproductive success of both sexes is Poisson (Eq. B10).
- (7) An adjustment to Reed et al. (1986), in which Poisson reproductive success is not assumed (Eq. B11).
- (8) Lacy & Clark (1989), who suggested an adjustment for population fluctuations (Eq. B12) in estimating N_e for black-footed ferrets (*Mustela nigripes*).
- (9) An alternative adjustment for fluctuating population size (Eq. B13) of Crow & Kimura (1970, p. 360).

Results

Basic Simulation Runs and N_e

Mean N_e/N for hypothetical grizzly bear populations calculated from the 50 replicate runs by our pedigree analysis method varied from 0.241 (68% confidence limits 0.203–0.295) for a population with our estimated values for male mating, hunted under a "chance" hunting regime, to 0.324 (68% confidence limits 0.275–0.394) for a trophy-hunted population with our estimated values for male mating. As expected from theory, increasing the variance of reproductive success among males reduced N_e/N (Table 3).

Estimated N_e from Demographic Formulas

Table 4 summarizes demographic data used in estimating N_e using published formulas. The Hill (1972) formula predicted N_e among the six basic runs accurately, generally overestimating N_e by approximately 5% (Table 3). Hill made no allowance for fluctuating population size, while our simulated populations had standard deviations approximately 10% of their long-term average numbers. Covariances in production of male and female lifetime surviving offspring, used only in the Hill formula, were generally much lower than variances along any of the four pathways for gametes (mother-daughter, mother-son, father-daughter, father-son). Because polygyny affects reproductive heterogeneity among males more than among females (Wood 1987), variances along the male pathways, as well as male co-

Table 3. Effective population size as a function of total census number (N_e/N), as estimated by our simulation model, and using published formulas based on demographic data.

Simulation										
Hunt	Male mating	Eq. 4 ^a	Hill ^b	Ryman ^c	Ryman ^d	Ryman ^e	Lemkuhl ^f	LaCava ^g	Reed ^h	Reed ⁱ
None	Random	0.311	0.334	0.431	0.372	0.344	0.055	0.974	0.514	0.322
None	Extreme	0.265	0.274	0.431	0.372	0.291	0.053	0.914	0.434	0.225
None	Estimated	0.285	0.304	0.431	0.372	0.326	0.054	0.961	0.494	0.283
Random	Estimated	0.324	0.308	0.425	0.363	0.317	0.045	0.970	0.520	0.291
Chance	Estimated	0.241	0.255	0.405	0.352	0.274	0.058	0.946	0.455	0.238
Trophy	Estimated	0.322	0.360	0.405	0.356	0.359	0.051	0.935	0.492	0.358

^a See methods section.

^b Eq. B1.

^c Ryman et al. 1981, assuming values used for moose: $N_{em}/N_m = 0.9 \times N_{ef}/N_f$, random survival of subadults.

^d Ryman et al. 1981, assuming values used for moose: $N_{em}/N_m = 0.9 \times N_{ef}/N_f$, 10% of subadult survival on family basis, 90% on random basis.

^e Ryman et al. 1981; N_{em} calculated from male data; all variances of lifetime offspring production computed directly from data.

^f Lemkuhl 1984; from Eq. B8.

^g LaCava & Hughes 1984; Eq. B9.

^h Reed et al. 1986; Eq. B10.

ⁱ Reed et al. 1986; adjusted for non-Poisson progeny distribution, Eq. B11.

variance, were generally greater than along the female pathways.

Under the assumption that N_e/N for males was 0.9 N_e/N for females, used for moose in their paper, the procedure of Ryman et al. (1981) overestimated N_e/N , more so when none of the subadult survival was assumed to be on a family basis. However, when Ryman's procedure was performed assuming knowledge of the male, as well as the female demographic parameters, and when V_k was computed directly for each sex rather than with the equations of Crow & Morton (1955), results were closer to the actual N_e/N values. The average deviation from the true N_e among the six population variants was less than 10%. All values overestimated N_e/N , and all but one were higher than the corresponding

estimate of Hill. The two formulas are similar, but Ryman's omits the covariance terms, which were always positive, leading to slight overestimation of N_e .

Lemkuhl's (1984) formula always produced substantial underestimation of the true N_e . LaCava & Hughes's (1984) formula produced similarly large overestimations of N_e . Some speculations on the causes of error in Lemkuhl's procedures are presented in the "Discussion" to follow.

Reed et al.'s (1986) estimation procedure overestimated N_e/N , usually by roughly 60%. However, when adjusted for non-Poisson distribution of surviving offspring, the modified Reed formula performed about as well as the Hill formula. We also computed Reed's formula using a single, pooled estimate of generation inter-

Table 4. Selected demographic statistics relevant to estimation of N_e from the 6 basic simulation runs.

	Type of Hunt					
	Male Mating System					
	None Random	None Estimated	None Extreme	Random Estimated	Chance Estimated	Trophy Estimated
<i>Census population:</i>						
Mean number	102.8	102.8	102.8	95.3	97.4	92.7
Coefficient of variation	9.9%	9.9%	9.9%	11.6%	8.0%	10.5%
Mean age, males	3.0	3.0	3.0	3.5	2.3	1.5
Mean age, females	7.4	7.4	7.4	6.6	7.7	7.6
Proportion Males:Females	43:57	43:57	43:57	46:54	43:57	42:58
<i>Breeding population:</i>						
Generation interval (L)						
Males	10.1	11.5	11.4	11.7	11.0	7.4
Females	10.1	10.1	10.1	10.0	10.1	9.7
Proportion Males:Females	42:58	40:60	35:65	41:59	38:62	38:62
Recruited yearly						
Males	2.2	1.8	1.3	1.8	1.6	2.5
Females	3.3	3.3	3.3	3.0	3.0	3.1
Variance in lifetime distribution of contributing progeny						
Males	6.3	8.2	10.3	7.4	11.0	4.2
Females	2.8	2.5	2.2	3.3	2.3	3.3

val (as in Hill), rather than the separate estimates. Differences in the resulting N_e estimates varied from none, under random male mating with no hunt, to 5% of the estimate under trophy hunting (in which the generation interval for females was 31% greater than for males).

Among those models most closely tracking N_e , overestimation was more common than underestimation. Our simulated populations fluctuated slightly, but only the Lemkuhl formula, which never gave reasonably correct results, included an explicit correction for nonconstant population size. In the experimental population with high fluctuations, the overestimation was more pronounced, as expected. The corrections suggested by Lacy & Clark (1989) and Crow & Kimura (1970) reduced N_e/N values estimated by Equations B1, B3, and B11 to much closer to the true N_e value (Table 5).

Discussion

N_e Estimators

For management purposes, it is probably unnecessary to strive for great precision in N_e estimates. Given the likely uncertainties in data necessary for its calculation by any method, excessively rigid dependence on even the best of estimations is unwarranted. Also, other factors may operate to change the rate of loss of genetic diversity from that predicted from N_e (e.g., selection, migration, mutation, avoidance of close inbreeding). At best, N_e estimates can provide managers with an approximation of the degree of genetic loss likely to take place. Nonetheless, the estimator of LaCava & Hughes (1984) and the unmodified estimator of Reed et al. (1986) are likely to paint an overly optimistic picture for most populations of large mammals. Similarly, the Lemkuhl (1984) procedure is likely to create more pessimism than is appropriate, possibly leading wildlife

managers, many of whom already possess a great deal of skepticism regarding the importance of maintaining genetic diversity, to dismiss the issue entirely.

When accurate parameter estimation is possible, the Hill (1972), Ryman et al. (1981), and modified Reed et al. (1986) formulas all appear to predict N_e values well. When parameters for males are not available, the accuracy of the Ryman estimate depends greatly on the estimates used for the ratio of N_{em}/N_m to N_{ef}/N_f and the ratio N_m/N_f . An estimate must also be made of the proportion of pre-adult mortality that occurs on a family basis. Ryman et al. (1981) used zero and 10%. Shull & Tipton (1987) in a recent application of Ryman's procedure for American bison (*Bison bison*), used zero and 30%. In our simulated bear populations, most mortality occurred after cubs had left their mother but before they became reproductively active, and was therefore random. However, a small portion was known to occur on a family basis, because litters that had lost their mother prior to the usual weaning age were immediately exposed to much higher mortality rates. We would have been hard-pressed to estimate the relative magnitudes of these two types of subadult mortality prior to running the simulations, despite our knowledge of the simulation's parameters. On the other hand, if heritability of fertility is thought to be present and can be estimated, the Ryman formula provides for this parameter. However, neither the Ryman nor Reed formulas include the covariance terms, which could influence N_e in species with different subadult mortality patterns than our simulated bears.

Two additional estimators, not treated here, deserve mention. Recently, Crow & Denniston (1988) provided new derivations for both N_{et} and N_{ev} of populations with discrete generations, and clarified differences between the two types of N_e . Both estimators included the covariance terms as defined by Hill (1972). They pointed out, however, that their estimator for N_{ev} reduced to approximately the Hill formula for overlapping generations if population size could be assumed to be constant. Although our simulated populations were not strictly constant (yearly numbers varied randomly about the long-term mean due to demographic stochasticity), they were intended to represent equilibrium conditions, and thus the constant size assumption was not grossly violated. Application of Crow & Denniston's formula (modified to reflect overlapping generations) to our simulated data yielded estimates within 2% of estimates using Hill's equation (Table 5).

Lande & Barrowclough (1987) also reviewed estimation and application of N_e for population management, suggesting methods to incorporate the various non-ideal population characteristics. We found their methods unwieldy when applied to simulated grizzly bear populations, and judged that some of the simpler equations we assessed provided estimates whose accuracy was well

Table 5. N_e/N for a simulated grizzly bear population with high yearly population fluctuations, as estimated by 3 demographic formulas, with and without adjustments for nonconstant population size. The mean N_e value calculated using Eq. 4 was 0.234.

	Uncorrected	Corrected for fluctuations in numbers	
		Lacy & Clark ^a	Crow & Kimura ^b
Hill (1972)	0.286	0.189	0.206
Ryman et al. (1981) ^c	0.307	0.203	0.228
Reed et al. (1986) ^d	0.284	0.186	0.204

^a $N_e = N_e / (1 + CV^2)$, where CV = coefficient of variation in yearly numbers of breeders.

^b $N_e = N_e - (\sigma^2/N)$, where σ^2 = variance in yearly numbers of breeders.

^c All values computed directly (Eq. B3).

^d Modified to adjust for non-Poisson variance in lifetime production of contributing offspring (Eq. B11).

within the resolution of data likely to be collected for such populations in the field.

Variables Affecting N_e

Many authors have emphasized the importance of population fluctuations in reducing N_e from N (e.g., Hartl 1980). Our modeled grizzly bear populations fluctuated little, generally with a standard deviation of 10% or less of the mean population size. At this level of variation, population fluctuations were a minor contributor to the reduction of N_e relative to N . The adjustments of Crow & Kimura (1970) and that used by Lacy & Clark (1989) reduced the magnitude of underestimation slightly. We suspect that most populations of 'k-selected' large mammals show similarly modest yearly fluctuations.

The Hill (1972) and Crow & Denniston (1988) formulas included covariance terms for progeny distributions. In an analytical treatment, Wood (1987) found that covariances were potentially important components to the overall N_e estimate. However, our results suggest that, at least for our hypothetical grizzly bears, the covariances were relatively minor factors because they were small relative to the variances. Wood (1987) similarly found that covariance terms for a human population were considerably smaller than variance terms.

Some confusion arises in applying formulas for which an estimate of generation interval is required, over whether a pooled average or separate estimates for each sex are most appropriate. Our results with the Reed et al. (1986) formula suggest that, at least for grizzly bears, it makes little difference. Even when sex-specific generation intervals were maximally different, resultant estimates were within 5% of each other.

Another source of possible confusion surrounds the definition of adulthood, which is needed in most calculations. Ryman et al. (1981) specify adults as those attaining reproductive age, while Reed et al. (1986) require breeding as well. The analogous problem exists in defining k and V_k , that is, the mean and variance of lifetime reproductive output can be viewed as applying to all animals reaching a specified age, or only to animals that contribute at least one offspring. Our results lend support to the suggestion of N. Ryman (personal communication 1986) that the two approaches yield similar estimates as long as consistency in definition is maintained. That is, if adults are defined as those attaining a minimum breeding age, k and V_k of those adults must be defined as the mean and variance of numbers of their offspring attaining that age. If adults are defined as those actually contributing to subsequent generations, k and V_k must be defined as the mean and variance of their offspring who themselves become contributors.

In general, slight discrepancies in definition of terms were less important to the accuracy of a formula than was failure to include an important demographic con-

sideration. Variance in lifetime production of surviving progeny was a crucial parameter; the unmodified Reed formula overestimated N_e because it ignored the possibility of non-Poisson variance. When corrected, the Reed formula gave results virtually indistinguishable from the Hill formula. Overlapping generations was an important consideration; the LaCava & Hughes formula produced wild overestimates because it ignored both overlapping generations and non-Poisson variance.

The formula of Lemkuhl (1984) included all these critical demographic parameters yet failed to produce accurate estimates. Lemkuhl's adjustment for non-Poisson variance of lifetime surviving offspring born to females (Eq. B4, Lemkuhl's Eq. 3) apparently underestimates N_e . The adjustment for nonconstant population size produces an additional underestimate (compare Eq. B7 with adjustments of Lacy & Clark [Eq. B12], and Crow & Kimura [Eq. B13]). Finally, to adjust for overlapping generations, Lemkuhl suggests that N_e is generally one-half the corresponding N with nonoverlapping generations. This rule of thumb appears reasonable when applied to our simulated grizzly bear populations (Table 5). However, Lemkuhl states that this adjustment must be made to the number of *breeding* animals (p. 172), thus requiring yet an additional adjustment to arrive at N_e/N if N is defined as the entire census population. The adjustments for overlapping generations made by the Hill, Crow & Denniston, Ryman, and Reed formulas implicitly account for the fact that not all animals are breeders. Thus Lemkuhl adjusts for overlapping generations twice, further contributing to the negative bias of his estimate.

Application of Results

To estimate N_e for a wild population using a published formula, reasonably accurate demographic data are needed. The likely sticking point with any formula is estimating the variance in progeny distribution terms from field data, to say nothing of the covariance terms. As Wood (1987) pointed out, these terms are also vulnerable to misinterpretation. Wood (1987) recently provided a method for estimating all these terms for use in the Hill formula, using data on a tribe in Papua New Guinea. However, he had access to detailed paternity records, data rarely available for wild populations. We agree with Wood (1987), however, that these variance terms can be exceedingly important in estimating N_e , and should not be omitted.

An alternative that may be useful in some cases is simulating population dynamics and calculating such parameters directly from the results for input into the accurate formulas (e.g., Hill). Our simulation model allowed us to derive estimates for the variances and covariances in progeny distributions given life table data and estimates of likely breeding success enjoyed by

Table 6. Mean reproductive parameters for female grizzly bears in the simulation model.

	Years			
Age at 1st reproduction:	5	6	7	8
Percent:	65%	26%	9%	1%
Mean age at 1st reproduction:	5.50 years			
	Cubs			
Litter size:	1	2	3	
Percent:	19%	55%	26%	
Mean litter size:	2.07 cubs			
	Years			
Breeding interval:	2	3	4	5
Percent:	14%	63%	20%	2%
Mean breeding interval:	3.09 years			
Mean cubs/reproductive female/year:	0.67			

males of differing ages. Alternative simulation structures might allow biologists to estimate the likely breeding success for males on the basis of different dominance rankings, how long dominance is maintained by individuals, and how dominance translates into breeding success. Admittedly, data with which to estimate these parameters are also rarely available. However, we have found that field biologists may be willing to make educated, insightful guesses for these parameters, whereas their ability to estimate such opaque parameters as, for example, the covariances needed in the Hill and Crow and Denniston formulas is questionable. Our procedure

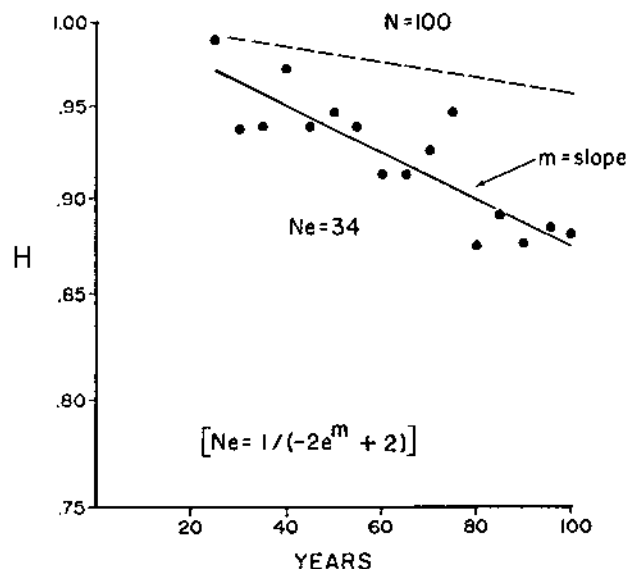


Figure 1. Least squares fit of the natural log of heterozygosity (H) on time (slope = m) from a randomly selected simulation with no hunting and random male mating. The dashed line represents the expected rate of loss of heterozygosity for an ideal population of 100 bears.

involved polling knowledgeable bear biologists about reproductive success of males, following a thorough discussion of the structure of our simulation model. Our simulation results then alleviated the need to make any additional assumptions regarding variances of reproductive success.

The simulation we developed also permitted estimation of N_e directly through a measure of the relatedness of all individuals. Our procedure gave an estimate that reflected the exact demographics of each particular run, and as such, required replicating a number of times to determine the expectation of N_e . The Hill estimate from a single run was a better predictor of the ultimate average N_e from all 50 runs than was the N_e from any single run, suggesting that it may use information more efficiently than our approach using pedigree analysis, or be less susceptible to sampling error. However, our approach also allowed the estimation of confidence limits for N_e , which themselves may have management utility. Confidence limits remind us that even the best estimate of N_e is only an expectation; stochastic variations in demographic events can easily alter the rate of genetic loss from that expected.

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Appendix A: Simulation Model Parameters

Natality and survival rates came from data on un hunted populations in Glacier National Park, British Columbia (Mundy & Flook 1973); Glacier National Park, Montana (Martinka 1974); and Yellowstone National Park (Craighead et al. 1974; Knight & Eberhardt 1984); as well as hunted populations in southeastern British Columbia (McClellan 1983) and northwestern Montana (Jonkel 1982; Aune & Stivers 1983). Our intent was not to mimic the behavior of a particular population, but rather to create a "representative" grizzly bear population of the North American Rocky Mountains by combining data from ecologically similar areas. The resulting model was similar in natality rates (Table 6) and age-structure characteristics to other published grizzly bear

simulation models (McCullough 1981; Knight & Eberhardt 1985). Further descriptions of the stochastic model and rates used are available in Harris (1984) and Harris & Metzgar (1987).

Appendix B: Published Formulas for Estimation of N_e

Hill (1972)

$$1/N_e = 1/16ML[2 + \sigma_{mm}^2 + 2(M/F)\text{cov}(mm,mf) + (M/F)^2\sigma_{mf}^2] + 1/16FL[2 + (F/M)^2\sigma_{fm}^2 + 2(F/M)\text{cov}(fm,ff) + \sigma_{ff}^2] \quad (\text{B1})$$

where M,F = number of males (or females) breeding yearly, L = average age of all parents, σ^2 = variance of number of progeny. Subscript mm denotes male progeny from fathers, mf female progeny from fathers, fm male progeny from mothers, and ff female progeny from mothers, $\text{cov}(mm,mf)$ = covariance in male and female progeny from fathers, and $\text{cov}(fm,ff)$ = covariance in male and female progeny from mothers. We interpreted M and F as the yearly number of new contributors to the subsequent generation (not merely those attaining reproductive age), and the variances and covariances of total progeny as pertaining only to those offspring who themselves become contributors.

Ryman et al. (1981)

$$\hat{N}_e = (N'L) / \{(1 + 3h^2)(V_{ka}/k_a^2) + (1/k_a)\} \quad (\text{B2})$$

where \hat{N} = annual recruitment of females of breeding age, L = mean age of mothers, h = heritability of fertility, and k_a and V_{ka} = mean and variance of individual lifetime production of offspring who themselves survive to reproductive age (a = adult).

Ryman et al.'s (1981) simulation model did not include males; they assumed for moose

$$N_e(\delta)/N(\delta)/N_e(\varphi)/N(\varphi) = 0.9$$

and

$$N(\delta)/N(\varphi) = 0.67$$

To calculate N_e for sexes combined,

$$N_e = 4\hat{N}_{e\delta}\hat{N}_{e\varphi}/(\hat{N}_{e\delta} + \hat{N}_{e\varphi}) \quad (\text{B3})$$

In addition, their model did not provide data with which to estimate V_{ka} directly. Rather, they estimated the mean (k) and variance (V_k) of individual lifetime production of newborns, and converted to V_{ka} assuming alternatively random survival of offspring to adulthood, and 10% of survival being on a family basis (Crow & Morton 1955).

Lemkuhl (1984)

The number of breeding animals required to achieve $N_e = 50$:

$$N_1 = (2N_e V_k + 1)/k^2 \quad (\text{B4})$$

where k and V_k are defined as by Ryman et al. (above). To account for imbalanced sex ratio:

$$N_2 = N_1 * \{[4N_m N_f / (N_m + N_f)]/N\} \quad (\text{B5})$$

where N_m and N_f are numbers of breeding males and females, respectively. To account for overlapping generations:

$$N_3 = N_2 * 2 \quad (\text{B6})$$

To adjust for population fluctuations:

$$N_4 = N_3 * (N_{max}/N_{min}) \quad (\text{B7})$$

where N_{max} and N_{min} are maximum and minimum population levels. Finally, if the total number of animals (rather than just the number of breeders) is to be calculated:

$$N_5 = N_4 * (1/p) \quad (\text{B8})$$

where p is the proportion of the total population made up by breeding animals.

LaCava and Hughes (1984)

$$N_e = 4m(1 - m)N \quad (\text{B9})$$

where m = the proportion of males among adults. This is equivalent to the more common

$$1/N_e = 1/(4N_m) + 1/(4N_f)$$

originally put forward by Wright (1931).

Reed et al. (1986)

$$1/N_e = 1/(4L_m M_b k_m l_m) + 1/(4L_f F_b k_f l_f) \quad (\text{B10})$$

where L = generation length, M_b and F_b = number of breeding males and females, respectively, k = number of young born to each sex each year, l = probability that a newborn of each age survives and reproduces, and subscripts m and f = male and female, respectively.

Reed et al. (1986), Adjustment

Although not in their paper, Reed (personal communication, 1987) suggested that their formula could be adjusted to account for non-Poisson variance in lifetime progeny distribution by multiplying the final expression by:

$$k/((k - 1) + (V_k/k)) \quad (\text{B11})$$

where k and V_k take the values appropriate when offspring are considered only if they become contributors.

Lacy & Clark (In Press)

To adjust for population fluctuations,

$$N_e = N_e / (1 + cv^2) \quad (\text{B12})$$

where N_e = effective population size calculated assuming constant population size, and cv = coefficient of variation of adult population size (which we interpreted as number actually contributing yearly).

Crow & Kimura (1970)

An alternative adjustment for population fluctuations,

$$N_e = N_e - (\sigma^2/N) \quad (\text{B13})$$

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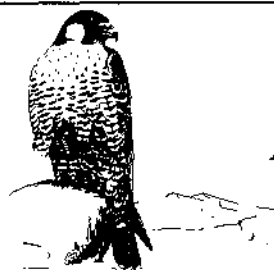
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