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Effective sizes of livestock populations to prevent a decline in fitness

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Abstract In livestock populations, fitness may decrease due to inbreeding depression or as a negatively correlated response to artificial selection. On the other hand, fitness may increase due to natural selection. In the absence of a correlated response due to artificial selection, the critical population size at which the increase due to natural selection and the decrease due to inbreeding depression balance each other is approximately $D/2\sigma^2_{wa}$, where D=the inbreeding depression of fitness with complete inbreeding, and σ^2_{wa}=the additive genetic variance of fitness. This simple expression agrees well with results from transmission probability matrix methods. If fitness declines as a correlated negative response to artificial selection, then a large increase in the critical effective population size is needed. However, if the negative response is larger than the response to natural selection, a reduction in fitness cannot be prevented. From these results it is concluded that a negative correlation between artificial and natural selection should be avoided. Effective sizes to prevent a decline in fitness are usually larger than those which maximize genetic gain of overall efficiency, i.e., the former is a more stringent restriction on effective size. In the examples presented, effective sizes ranged from 31 to 250 animals per generation.

Key words Critical effective population size
Inbreeding depression · Natural selection · Fitness
Conservational biology

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Introduction

New developments in animal breeding schemes are designed to increase genetic gain, but inbreeding rates are often increased concomitantly. For example, the introduction of BLUP as a means of estimating breeding values (Henderson 1984) and of MOET nucleus schemes (Nicholas and Smith 1983) will increase annual rates of inbreeding because (1) the weightings attached to pedigree information are increased, (2) generation intervals are decreased, and (3) because of selection within small nucleus populations in the case of MOET schemes. The question arises, what rate of inbreeding is justifiable in a breeding scheme. Restricting rates of inbreeding may have a major impact on the optimization of breeding schemes. For instance, mass selection can be superior to BLUP selection when the constraint on inbreeding is severe (Quinton et al. 1992).

Detrimental effects of inbreeding are: (1) the reduction of additive genetic variance, which reduces rates of response and limits to selection for the trait under selection and other traits; (2) inbreeding depression for the trait under selection, if gene effects are non-additive; (3) inbreeding depression in fitness of the animal. However, in his simulation of dairy cattle breeding, Meuwissen (1989) found that reduction in additive genetic variance, over ten generations of selection, would only reduce total genetic gain by 13%. It was assumed, that the effective population size (N_e) was small (ten animals), the accuracy of selection was high (about 0.8), and the proportion selected was small (0.1). These assumptions reduce cumulative genetic gain more than is likely in practice. In this rather extreme situation, doubling the N_e increases the rate of gain by approximately 6.5%.

Because most production traits, such as growth rate and feed efficiency, do not show a high degree of inbreeding depression (Falconer 1981), inbreeding depression is not a major factor for production traits. In contrast, fitness, a combination of survival and reproductive traits, is often not selected for directly but is highly influenced by inbreeding depression (e.g., Beilharz 1982; Wiener et al.

1992c). Hence, in the medium term, the most stringent restriction on the rate of inbreeding is imposed by inbreeding depression of fitness.

Rates of deterioration of fitness traits through selection were derived by Robertson (1966). These rates may be ameliorated by incorporating them in selection indices, e.g., by desired gains indices (Cunningham et al. 1970). This strategy requires the measurement of components of fitness and knowledge of their relative importance for fitness and of their genetic parameters. On the other hand, N_e may be chosen such that depression of fitness due to inbreeding equals the additive genetic improvement due to natural selection, so that fitness should not change. Thus, Soulé (1980) considers natural selection as the remedy against the fixation of deleterious alleles, while Franklin (1980) and Soulé (1980) provide crude empirical values of minimal viable effective population sizes.

The aim of the present paper is to assess the critical effective population size for which decrease of fitness due to inbreeding depression and increase of fitness due to natural selection balance one another. The perspective of animal breeders is rather short term so that the accumulation of new mutations is ignored. Accumulation of mutations affects the long-term genetic variance and thus the response (Hill 1982) and the time till extinction of populations due to mutational meltdown (Lynch and Gabriel 1990). A simple formula, which ignores the effects of selection on genetic variances (Bulmer 1971) is derived. More complicated models are compared to the simple formula.

Materials and methods

A population with discrete generations is assumed which is subject to artificial selection. Not all animals have maximum fitness, so that variation for fitness exists, which is partly due to additive and partly due to dominant gene effects. Epistatic gene interactions are assumed to be absent. Let N_m be the total number of male parents with n_{mi}, the number of offspring produced by the ith male parent. Fitness is defined as $w_{mi}=n_{mi}/\bar{n}_m$, where $\bar{n}_m=\Sigma n_{mi}/N_m$ is the average number of offspring per male parent. Note that average fitness is $\Sigma w_{mi}/N_m=1$. Fitness of female parents is defined similarly. Thus, artificial selection precedes natural selection within a generation and fitness is treated as a maternal/paternal trait. If production traits undergoing artificial selection are genetically uncorrelated to fitness then gene frequencies and genetic variances are expected to remain unchanged by artificial selection (except as influenced by effective population size which is affected by intensity of selection).

A simple formula for critical effective population size

The fundamental theorem of Fisher (1929) states that the expected increase in fitness through natural selection on viability is σ^2_{wa} per generation, where σ^2_{wa} is the additive genetic variance of fitness. This conclusion may be drawn from the following argument. The phenotypic selection differential of male parents is the fitness of male parents minus the population mean of 1 weighted by their number of offspring:

$$X_{Sm}=\Sigma(w_{mi}-1)w_{mi}/N_m=\Sigma(w_{mi}-1)^2/N_m+\Sigma(w_{mi}-1)/N_m=V(w_{mi}).$$

The same holds for female parents, so that $X_{Sf}=V(w_{fi})$.

If the mating of parents is at random with respect to fitness, then, from regression theory, the increase in breeding value for fitness is given by $\frac{1}{2}[X_{Sm}\ V(w_{am})/V(w_m)+X_{Sf}\ V(w_{af})/V(w_f)]=\sigma^2_{wa}$, where $V(w_{ax})$=the additive genetic variance of fitness in sex x, and $\sigma^2_{wa}=\frac{1}{2}[V(w_{am})+V(w_{af})]$. Thus, the expected increase in relative fitness through natural selection is σ^2_{wa} per generation. This derivation invokes *linear* regression of genotypes on phenotypes, which practically implies multi-normality, i.e., the infinitesimal model and normal distributed environmental effects. However, because selection differentials due to natural selection are small, predictions from linear regression will hold approximately even if distributions are nonnormal and do not exhibit linear regression, e.g., in the case of genetic models with few loci. Jacquard (1972) shows that the theorem is approximately correct even for the one-locus model.

In generation t, the increase of inbreeding depression is $(F_t-F_{t-1})D$, where F_t is the inbreeding coefficient at generation t and D is the depression of fitness in percentages of the mean per percent of inbreeding. If ΔF is the rate of inbreeding as defined by Falconer (1981), this increase per generation is $\Delta F(1-F_{t-1})D$. With an additive genetic model, increase in fitness due to natural selection in generation t is $(1-F_{t-1})\sigma^2_{wa}$. Hence, two forces, natural selection increasing fitness and inbreeding depression reducing fitness, balance if $\sigma^2_{wa}=\Delta F\,D$, i.e., if effective population size is $N_e=D/2\sigma^2_{wa}$, because $\Delta F=1/2N_e$. But, if inbreeding depression occurs, the genetic model clearly includes dominance.

The following argument suggests that, even with dominance, an effective population size of $D/2\sigma^2_{wa}$ would prevent a decline of fitness in later generations. Increase of fitness due to natural selection, as derived above, is the sum of the covariances between sire and offspring and that between dam and offspring. The covariance between parent and offspring is derived for a model that includes dominance and inbreeding in Appendix 1. Appendix 1 shows, that for traits with low heritabilities, high coefficients of variation, and high inbreeding depression, which is generally the case for fitness traits, the covariance between parent and offspring exceeds $\frac{1}{2}(1-F_t)\sigma^2_{wa}$, where again ΔF is assumed to be small. Hence, increase in fitness would exceed $\sigma^2_{wa}(1-F_t)$ and $D/2\sigma^2_{wa}$ is a conservative estimate of the critical effective population size.

The two forces, inbreeding depression decreasing average fitness and natural selection improving additive genetic value, are assumed to be additive. In view of the complex nature of the stochastic process of changing gene frequencies, this approximation will be tested against results from transmission probability matrices describing the evolution of gene frequency distributions (Narain and Robertson 1969).

Let A_1 and A_2 denote the positive and negative allele for fitness, respectively. In generation t, the frequency of A_2 is q_t. Further the relative fitnesses of genotypes A_1A_1, A_1A_2 and A_2A_2 are (1+a), (1+d), and (1–a), respectively. Gametes of selected animals are assumed to unite at random, hence, the frequencies of the genotypes are $(1-q_t)^2$, $2q_t(1-q_t)$, and q_t^2, respectively. The frequency of A_2 after selection is $s^*(q_t)=[q_t{}^2(1-a)+q_t(1-q_t)(1+d)]/[q_t{}^2(1-a)+2q_t(1-q_t)\cdot(1+d)+(1-q_t)^2(1+a)]$. The denominator is the mean fitness.

A monoecious population of size N is assumed which has a probability of selfing of 1/N, and hence $N=N_e$. Let p_{it} be the probability that the frequency of A_2 is $i/2N$ at generation t, for $i=0,..,2N$. The vector p_t contains the elements p_{it}. If $q_t=j/2N$ in generation t, $q_{t+1}=i/2N$ with probability T_{ij}. From the binomial distribution:

$$T_{ij}=\binom{2N}{i}[s^*(j/2N)]^i\,[1-s^*(j/2N)]^{2N-i}.$$

If T denotes the matrix with elements T_{ij}, the evolution of the distribution of gene frequencies is given by the recurrence relationship: $p_{t+1}=Tp_t$ (Narain and Robertson 1969) from which the evolution of the distribution of gene frequencies can be obtained given an initial distribution; here: $q_0=0.2$ will be used.

Correlation between fitness and production and variance reductions

If a correlation exists between fitness and production, then here this correlation will be assumed to be negative. This assumption is made because (1) only negative correlations cause a problem if decline in fitness is to be prevented, and (2) negative correlations are more likely as the resources of an animal are limited and merit in one trait may be (partly) offset by demerit in another; hence, the assumption that selection for production will most likely lead to a correlated decrease in fitness. Because selection for production precedes selection for fitness, reduction in σ^2_{wa} due to selection will need to be accounted for. The $1-F_t$ terms in the expressions for reduction in variance and inbreeding depression cancel as shown in the previous section. The non-additive genetic terms will be ignored which will lead to conservative estimates of response to natural selection (see Appendix 1).

In the following, genotypes for fitness and production will be assumed to involve many alleles such that the genotypic distributions are approximately normal. Let $C(i,j)_t$ be the (co)variance between trait i and j in generation t, where i (j) is P_p, P_a, W_p, or W_a, which are the phenotypes and additive genotypes of production and of fitness, respectively (if i=j, the variance of i is denoted). Further, * denotes after selection for production. For simplicity, sires and dams are assumed to be identically selected. Extension to differential sire and dam selection is straightforward. From regression theory (Pearson 1903):

$$C(i,j)_t^*=C(i,j)_t-C(i,P_p)_t\,C(j,P_p)_t\,k_p/C(P_p,P_p)_t,$$

where k_p is the reduction in variance of $C(P_p,P_p)_t$. For truncation selection $k_p=i_p(i_p-x_p)$, where i_p and x_p are the standardised selection differential and truncation point, respectively. The correlated response of fitness is:

$$\Delta w_{pt}=i_p\,C(P_p,W_a)_t/\,C(P_p,P_p)_t.$$

Let $\bar{w}$ denote the average fitness after selection for production:

$$\bar{w}=1+\Delta w_{pt}.$$

The selection differential of fitness due to natural selection is obtained by weighting the fitness of the selected animals minus the mean of the selected animals by their number of offspring:

$$\Sigma w_i(w_i-\bar{w})/(\bar{w}\,N)=\Sigma(w_i-\bar{w})^2/(\bar{w}\,N)+\Sigma(w_i-\bar{w})/N=C(W_p,W_p)_t^*/\bar{w}.$$

The regression coefficient of W_a on W_p is $C(W_a,W_p)_t^*/C(W_p,W_p)_t^*$. The genetic response due to natural selection equals the selection differential times the regression coefficient:

$$\Delta w_{wt}=C(W_a,W_p)_t^*/\bar{w}.$$

Let $C(i,j)_t^{**}$ denote (co)variances of parents weighted by their number of offspring, because these (co)variances determine the (co)variances due to parents observed among the offspring. Again applying regression theory:

$$C(i,j)_t^{**}=C(i,j)_t^*-C(i,W_p)_t^*C(j,W_p)_t^*k_{wt}/C(W_p,W_p)_t^*.$$

As shown in Appendix 2, $k_{wt}=C(W_p,W_p)_t^*/\bar{w}^2$.

With identical male and female selection, the additive genetic (co)variances in the next generation are (Bulmer 1971),

$$C(i,j)_{t+1}=\tfrac{1}{2}C(i,j)_t^{**}+\tfrac{1}{2}C(i,j)_0,$$

where i (j) denote the additive genotypes of production or fitness. The second term represents variance due to Mendelian sampling. The phenotypic variances and covariances are obtained by:

$$C(r,s)_{t+1}=C(i,j)_{t+1}+C_E(r,s),$$

where r(s) denotes the phenotype corresponding to genotype i(j), and $C_E(r,s)$ is the environmental (co)variance of traits r and s.

This model will be used to investigate effects of variance reduction due to selection and correlated responses from artificial selection on the effective population size required to prevent fitness deterioration. Inbreeding depression and correlated response from artificial selection will decrease genetic values for fitness. Natural selection wil increase fitness. The critical effective population at which these effects balance will be compared to that predicted by $D/2\sigma^2_{wa}$.

Results

Comparing $D/2\sigma^2_{wa}$ to results from transmission probability matrix methods

Table 1 compares the population numbers for which the mean fitness is maintained at the initial level after ten generations of natural selection, using the transmission probability method. These results are compared to the prediction $D/2\sigma^2_{wa}=D/2h^2CV^2$. The ranges of coefficients of variation and heritabilities of fitness in Table 1 agree with the coefficients of variation and heritabilities of egg production in poultry and litter size in pigs and sheep (Smith 1984). With a coefficient of variation of 0.4, a fitness of w=0 is 2.5 standard deviations below the mean. Hence, a small proportion of the population would fail to produce offspring.

The values of gene effects a and d follow from the assumptions D=1, σ^2_{wa} (which is given in Table 1 as h^2CV^2), the initial gene frequency $q_0=0.2$, and the number of loci, L. The value of d is obtained as

$$d=D/2Lq_0(1-q_0), \tag{1}$$

and that of a as

$$\sigma_{wa}{}^2=2Lq_0(1-q_0)[a+d(2q_0-1)]^2, \tag{2}$$

which yields a quadratic in a with only one positive solution.

Table 1 The minimum effective population sizes to maintain fitness at its current level as derived from transmission probability matrices (N_e) compared with $D/2h^2CV^2$, where D=1 is the depression with complete inbreeding for different values of the positive homozygote (a) and the heterozygote genotype (d) at one locus. All loci are assumed to have equal a and d-values and initial gene frequencies of $q_0=0.2$

CV	h^2	No. of loci								
		20		40		80		160		
		a (×100)	N_e	a (×100)	N_e	a (×100)	N_e	a (×100)	N_e	$D/2h^2CV^2$
0.2	0.05	11.1	255	5.9	245	3.2	245	1.8	255	250
	0.10	11.9	120	6.5	115	3.6	120	2.1	125	125
0.4	0.05	12.9	55	7.2	55	4.1	60	2.4	60	63
	0.10	14.4	25	8.2	25	4.8	30	2.9	30	31
d (×100)		15.6		7.8		3.9		2.0		

Table 2 Critical effective population sizes (N_e) to maintain average fitness, when depression due to complete inbreeding D=1, phenotypic and genetic correlations between fitness and production are r, heritability and coefficient of variation of fitness are h_w^2 and CV, respectively, and the standardised selection differential and heritability of production, which is improved by mass selection, are i_p and 0.25, respectively. The results are proportional to D and are compared to $D/2\sigma_{wa}^2$

r	CV	h_w^2	N^e		$D/2\sigma_{wa}^2$
			$i_p=1$	$i_p=2$	
0.0	0.2	0.05	250	250	250
		0.10	126	126	125
	0.4	0.05	63	63	63
		0.10	32	32	31
–0.1	0.2	0.05	X[a]	X	250
		0.10	440	X	125
	0.4	0.05	130	>10000	63
		0.10	50	108	31
–0.2	0.2	0.05	X	X	250
		0.10	X	X	125
	0.4	0.05	X	X	63
		0.10	127	X	31

[a] X=the negative correlated response of artificial selection exceeds the natural selection response so that a decline in fitness cannot be prevented

The approximation $D/2\sigma_{wa}^2$ generally overestimates slightly the critical N_e (Table 1), as expected from Appendix 1. Overestimation is largest with small numbers of loci and with large σ_{wa}^2. Appendix 1 shows that in such situations contributions of non-additive terms to covariance between parent and offspring is largest. Increased covariance between parent and offspring implies more response from natural selection and, hence, a smaller critical population size.

If inbreeding depression is large and additive genetic variance is small, the effects of genes need to be overdominant to satisfy these conditions, i.e., d>a (see Table 1). This situation occurs particularly when the number of loci determining fitness is moderate or small. With overdominant gene action, selection tends to intermediate gene frequencies which are difficult to maintain, because drift leads to extreme gene frequencies, so that a large critical N_e is needed if gene effects are markedly overdominant.

Correlated response and reduction in variance due to selection

Table 2 provides the critical N_e after accounting for variance reduction due to selection and correlations between fitness and production. The results are for D=1, but results for different values of D can be obtained by multiplying the N_e of Table 2 by D.

If the correlations between fitness and production are zero, $N_e = D/2\sigma_{wa}^2$ is a good approximation for the critical N_e (Table 2). This indicates that reduction in variance due to natural selection is negligible, as expected for traits with low heritability. Natural selection cannot compensate for a negative correlated response of artificial selection, unless artificial selection is weak and the negative correlation is close to zero (Table 2). The critical N_e is markedly increased by a negative correlated response. If the correlated response exceeds the natural selection response, a decline of fitness (irrespective of the effective population size) cannot be prevented.

Discussion

The genetic model

Critical effective population sizes were obtained by balancing the effects of natural selection and inbreeding depression for a finite number of loci using a genetic model that encompassed non-additive genetic variation in the form of dominance but not epistasis. Depression was assumed to be proportional to the coefficient of inbreeding, which is a property of dominance but not generally of epistasis. Where this has been tested, dominance was the major cause of heterosis in between-line crosses but contributions of epistasis were significant for some traits (e.g., Abplanalph et al. 1984; Fairfull et al. 1987; Wiener et al. 1992a, b, c). The dominant effect of genes d is proportional to 1/L and the additive effect a is approximately proportional to $1/\sqrt{L}$ [see formulas (1) and (2)], hence, $\lim_{L\to\infty}$ d/a=0, i.e., gene effects are additive. Consequently, the number of loci was assumed to be finite.

When considering the genetic background of fitness, the effects of very rare recessive deleterious (or even lethal) genes are most striking. But such genes do not cause much additive variation of fitness. Therefore, and because the problems caused by these genes may be more efficiently tackled by genetic markers, the genetic model used here was not directed in particular towards such genes. Genes with smaller detrimental effects on fitness are more likely to increase in frequency and collectively lead to a substantial reduction in fitness. Also non-linearity of the heritability of fitness (Frankham et al. 1988; Frankham 1990) was not considered here. An average heritability weighted by the genetic contributions of the selection candidates was used.

Prevention of deterioration of fitness

In the introduction, the effects of inbreeding on fitness were argued to be a more stringent restriction on population sizes of livestock than inbreeding effects on production traits. Goddard and Smith (1990) maximized the genetic gain of economic efficiency by optimizing the number of bull sires selected. Reduction in genetic variance and depression of efficiency due to inbreeding were both considered. Goddard and Smith concluded that the optimum number of bull sires selected was ten bulls per generation, to be used equally (Poisson distribution of the number of offspring per bull). If Wright's (1931) formula, which ignores selection, is used and if the number of dams is infinite, an effective population size of 40 is obtained. This number is an overestimate, because the effect of selection on effective population size is large (Wray and Thompson 1990) and because the number of dams is finite. Further, it exceeds only the smallest effective sizes found in Table 2, i.e., those for CV=0.4 and h_w^2=0.1. Thus, preventing a decline in fitness would require more stringent restriction of effective population size than optimization of overall efficiency.

Goddard (1992) found an optimum number of bulls selected for the world-wide black and white cattle population of six per year, which is 30 per generation and an effective population size of 120 animals per generation using Wrights' (1931) formula. Because Wrights' formula overestimates effective population sizes substantially, this N_e remains smaller than the sizes presented in Table 1, except those in situations with high coefficients of variation.

Although some may doubt whether a change in fitness should be restricted to zero if selection is for overall efficiency there are reasons which make maintenance of fitness desirable. Clearly, the ability to survive and reproduce are vital, but some reduction may be compensated for by increased production. As fitness decreases its economic value will increase, which, ideally, will lead to a zero change at some critical value of fitness. Nevertheless, aloowing fitness to decline involves several risks: valuable genes may be lost; critical values of components of fitness may be overshot due to the time lags in the selection process; and unfit animals may lead to public concern about the production system and, eventually, to the decreased use of products. The trend towards larger farm sizes calls for more 'trouble free' animals. Prevention of a decline now, rather than be forced to address reduced fitness at some point in the future, seems reasonable.

The assumption has been made that a population has a desirable level of fitness at present and that any deterioration would be undesirable. This assumption may not hold immediately for populations that have been developed with large effective population sizes. In the short term, such populations may be maintained at lower N_e than $N_e=D/2\sigma_{wa}^2$. If fitness is considered too low, then larger effective population sizes would give an increase in fitness of approximately $(1-F_t)(\sigma_{wa}^2-D/2N_e)$.

The values of D and σ_{wa}^2

Assuming D=1, as in Tables 1 and 2, means that fitness will decrease to zero as inbreeding approaches 1. Values of D for major components of fitness are available from the literature and are usually between 0.5 and 1% of inbreeding depression per percent of inbreeding (e.g., Falconer 1981, p. 228; Woodard et al. 1982; MacNeil et al. 1989; Wiener et al. 1992c). Because of non-linearity and because inbreeding rates are low, inbreeding depression will be expressed per percent of inbreeding, which is denoted by δ. Because overall fitness is the product of its components, for instance overall fitness may be survival rate times litter size, the depression of overall fitness is larger than that of its components:

$\delta=1-\Pi_{\text{all } j}(1-\delta_j)$, which is for a small δ_j equal to $\Sigma_{\text{all } j}\,\delta_{j,}$

where δ and δ_j are the depression of overall fitness and the jth component of fitness per percent of inbreeding, respectively. If some components of fitness are neglected in this formula, D will be underestimated. Latter and Robertson (1962) and Beilharz (1982) also show that depression of overall fitness is substantially larger than that of the individual components.

The additive genetic effect of overall fitness is the product of the additive genetic effects of its component traits. Using a Taylor series approximation, the additive genetic variance is approximated by:

$\sigma_{wa}{}^2=\Sigma j\ CV_j{}^2h_j{}^2+\Sigma_j\Sigma_{ij}\ r_{ija}h_ih_jCV_jCVi,$

where CV_j $(h_j{}^2)$ is the coefficient of variation (heritability) of the jth component of fitness and r_{ija} is the additive genetic correlation between the ith and jth component. Neglecting components of fitness results in underestimation of both σ_{wa}^2 and D. Hence, the effect of neglecting components of fitness on the estimate of the critical N_e will depend on the specific situation.

The relationship between artificial and natural selection

It was assumed that high production could not compensate for low fitness and vice versa. In practical breeding schemes, natural selection response may be reduced by (1) greater management efforts to overcome low fitness of extreme producing animals, and (2) some standardization of family size if test places are limited. Whilst both these actions may tend to increase the critical effective population size required to maintain fitness, the effect of standardization of family size is more ambiguous because standardization also reduces the variance of family size and thus increases the effective population size.

Table 2 shows that natural selection can hardly compensate for a correlated response from artificial selection, which decreases fitness. Hence, a negative correlation between fitness and selection indices should be prevented to avoid decreasing fitness, which can be achieved by using desired gains indices (Cunningham et al. 1970). Probably, only the major components of fitness need to be included in the desired gains index. If some components, which have a negative correlation with the selection index are overlooked, they would become evident as selection proceeds and could then be included in the index. Natural selection will prevent deterioration of fitness components, which are uncorrelated to the selection index, if N_e is sufficiently large.

An implication of these considerations is the use of restricted indices. However Gibson and Kennedy (1990) suggest that restricted indices provide less genetic gain than unrestricted indices. Their conclusion assumes that a decrease in fitness may be compensated by an increase of production and that all influences on profitability are clearly identified and accurately costed. Moreover, a large decrease in fitness will lead to losses due to infertile or inviable animals which cannot be compensated by production, i.e., the profit function is non-linear. Goddard (1983) showed that non-linear profit functions are optimized by searching for the maximal profit that can be reached within the time horizon of the breeding plan, and then selecting with linear indices towards this optimum. He also showed that if a long-term perspective is taken and the population is at the optimum for, e.g., fitness, which may be approximately the case at the onset of selection, the optimal selection strategy is to maintain fitness at its optimum.

In conclusion, a simple formula was derived for the critical effective population size at which natural selection for fitness and inbreeding depression balance. The results agree with results from transmission probability matrices for genetic models with dominance and overdominance (Table 1). The effective size to accomplish this goal is generally larger than that obtained from maximizing the genetic gain of economic efficiency. Further, negative correlated response for fitness from artificial selection increased the required critical effective sizes substantially, and in some circumstances this deleterious response could not be offset by increasing population size. Hence, an effective population size of $D/2\sigma^2_{wa}$ is recommended and the correlation between fitness and the selection indices for production should be prevented from being negative.

The critical effective population sizes presented apply also to natural populations, where the critical effective population size is the minimum population size such that natural selection can make progress against inbreeding depression. Populations which are smaller than the critical size will presumably go to extinction as they enter a downward spiral of ever-decreasing fitness. The results also apply to conservation biology by providing the minimum sizes required for conservation of populations.

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Appendix 1

The genetic covariance between parent and offspring with dominance and inbreeding

Loci will be assumed independent; hence, variances and covariances at individual loci sum to the variances and covariances of genotypes. This implies that linkage disequilibria due to selection and small population size are neglected. Weir and Cockerham (1974) showed that linkage disequilibria may be large, but did not come to a general expression for the covariance between inbred individuals when accounting for this. The close agreement between effective population sizes with and without accounting for linkage disequilibria due to selection (Table 2) suggests that the effects of linkage disequilibria due to natural selection may be small. Further it is assumed that the rate of inbreeding is small, such that the inbreeding of the parent F_t is approximately equal to that of the offspring and to the coefficient of kinship φ_t.

In the base generation the genotypic effects can be decomposed into average effects and dominance deviations (Falconer 1981). (This decomposition of genotypic values is different from the values a and d used previously in the text but is more relevant to this particular problem.) From these V_A and V_D, the additive and the dominance variance respectively, can be defined; further define V'_D as the variance of dominance deviations for homozygotes; C'_{AD} as the covariance of the total average effect and dominance deviations of homozygotes; and D' the mean dominance deviation of homozygotes.

From the work of Gillois (1964) and Harris (1964) a general form for the covariance of two individuals i and j with genotypes G_i and G_j, descended from the same base generation, is given by:

$$\mathrm{Cov}\,(G_i,G_j)=2\varphi\,(i,j)\,V_A+2Q_3\,(i,j)\,C'_{AD}+Q_4\,(i,j)\,V'_D+H(i,j)V_D+I(i,j)D'^2,$$

where $\varphi\,(i,j)$=coefficient of kinship of i and j; $Q_n(i,j)$=probability that a random sample of n of the four genes from i and j are identical; $H(i,j)$=probability that neither i nor j are inbred but that i and j have two pairs of identical genes; $I(i,j)$=joint probability of i and j both being inbred minus the product of $F(i)$ and $F(j)$ [where $F(i)$=inbreeding coefficient of i].

If i is a parent of j, two of the four genes are obliged to be identical since a copy of one gene from i is passed to j. For simplicity these two genes will be termed ‘directly identical’. Then, $\varphi(i,j)=1/4(1+3F_t)$ since the probability of sampling the directly identical genes is $\frac{1}{4}$ and for all three of the remaining samplings the probability of identity by descent is approximately F_t, where F_t=average inbreeding coefficient in generation t. $Q_3(i,j)=\frac{1}{2}F_t(1+F_t)$ because with probability $\frac{1}{2}$, in a sample of three genes both directly identical genes are sampled and a third is identical with a probability F_t, and because in the remaining samplings none of the three genes are directly identical and the probability of identity is approximately ${F_t}^2$. $Q_4(i,j)={F_t}^2$ is straightforward. $H(i,j)=F_t(1-F_t)$ because the directly identical pair must be distinct from the other pair, which must be identical. Finally, $I(i,j)=0$ since the joint probability of being inbred equals approximately the product of the inbreeding coefficients ${F_t}^2$.

Therefore, the total covariance between parent and offspring is given by

$$\mathrm{Cov}_t(G_i,G_j)=\tfrac{1}{2}(1+3F_t)V_A+F_t(1-F_t)V_D+{F_t}^2V'_D+F_t(1+F_t)C'_{AD}.$$

This is the covariance between G_i and G_j with respect to the non-inbred base population and includes the covariance between any two individuals belonging to the same line. However, in livestock breeding the population under consideration is a single line. Therefore, the covariance of two randomly drawn individuals from the same line must be subtracted, i.e., $\mathrm{Cov}_t(G_i,G_k)$ where i and k have no specified relationship. In this case $\varphi(i,k)=F_t$, $Q_3(i,k)={F_t}^2$, $Q_4(i,k)={F_t}^3$, $H(i,k)=2{F_t}^2(1-F_t)$, and $I(i,k)=0$, and so

$$\mathrm{Cov}_t(G_i,G_k)=2F_tV_A+2{F_t}^2(1-F_t)V_D+{F_t}^3V'_D+2{F_t}^2C'_{AD}.$$

Table A1 The dominance variance without (V_D) and with complete inbreeding (V'_D), and the covariance between additive and dominant effects with complete inbreeding C'_{AD}. The depression with complete inbreeding is 1

No. loci	V_D	V'_D	Coefficient of variation			
			0.20		0.40	
			h^2=0.05	h^2=0.10	h^2=0.05	h^2=0.10
Additive genetic variance V_A:			0.002	0.004	0.008	0.016
			C'_{AD}:			
40	0.025	0.056	0.015	0.021	0.030	0.043
160	0.006	0.014	0.008	0.011	0.015	0.021

Therefore, the covariance of parent i with offspring j within lines is given by

$$\mathrm{Cov}_{wt}(G_i,G_j)=(1-F_t)[\tfrac{1}{2}V_A+F_{t(1-2F}t_{)V}D_{+F}t^2V'_D+F_tC'_{AD}]. \quad \text{(A1)}$$

All coefficients of non-additive terms contain F_t, hence, their contributions are small if inbreeding levels are low.

Values of V_D, V'_D and C'_{AD} for traits with small heritability and high coefficients of variation and inbreeding depression, as is the case for fitness traits, are shown in Table A1. Because $V_D<V'_D$ in Table A1, the sum of the second and third term of Eq. (A1) is positive for all F_t. Further, $C'_{AD}>0$, such that $\mathrm{Cov}_{wt}(G_i,G_j)>\frac{1}{2}(1-F_t)V_A$, so that $\frac{1}{2}(1-F_t)V_A$ may be used as a conservative underestimate of the covariance between parent and offspring.

Appendix 2

Reduction in variance due to natural selection

Artificial selection usually selects certain animals as parents and rejects others. Reduction in variance is then obtained by calculating variances of the selected parents. With natural selection, virtually all parents have offspring, but the numbers of offspring differ. Therefore, reduction in variance due to natural selection is obtained by weighting the parental values of the trait by the number of offspring. The relative number of offspring of selected parent i is w_i, which has mean $\bar{w}$ and variance V_w. It is assumed here that selection for production preceded natural selection, but the derivation also holds if there was no selection for production. Let X denote a trait after selection for production and X_i^* be the deviation of trait X from its mean, i.e., $E(X_i^*)=0$. Now, X_i^* is decomposed as:

$$X_i^*=b(w_i-\bar{w})+R_i,$$

where $b=\mathrm{Cov}(w_i,X_i^*)/V_w$. It is assumed that R_i does not depend on w_i, which will approximately hold for distributions close to normal. Hence, at least approximately, $E(R_i)=0$ and $\mathrm{Var}(R_i)=(1-r^2)V_X$, where r is the correlation between w_i and X_i^* and $V_X=\mathrm{Var}(X_i^*)$. The variance of X_{i*} when weighted by the number of offspring, i.e., accounting for natural selection, is:

$$\begin{aligned}
&\mathrm{Var}(X_i^{**})=\sum w_iX_i^{*2}/(\bar{w}\,N)-[\sum w_iX_i^*/(\bar{w}\,N)]^2\\
&=\sum w_i(w_i-\bar{w})^2b^2/(\bar{w}\,N)+\mathrm{Var}(R_i)-[\sum w_i(w_i-\bar{w})b/(\bar{w}\,N)]^2\\
&=\sum(w_i-\bar{w})^3b^2/(\bar{w}\,N)+\sum(w_i-\bar{w})^2b^2/N+\mathrm{Var}(R_i)\\
&-[\sum(w_i-\bar{w})^2b/(\bar{w}\,N)+(\sum(w_i-\bar{w})b/N)]^2.
\end{aligned}$$

The first term will be approximately zero if the distribution of w_i is approximately symmetric, i.e., the third central moment is approximately zero. In the last term $\sum(w_i-\bar{w})=0$, because the sum of deviations from the mean is zero. Hence approximately,

$$\begin{aligned}
&\mathrm{Var}(X_i^{**})=b^2V_w+\mathrm{Var}(R_i)-b^2V_w^{\,2}/\bar{w}^2\\
&=r^2V_X+(1-r^2)V_X-\mathrm{Cov}^2(w_i,X_i^*)/\bar{w}^2\\
&=V_X-\mathrm{Cov}^2(w_i,X_i^*)k/V_w,
\end{aligned}$$

where $k=V_w/\bar{w}^2$. Note that X_i can be w_i and the result will still hold with variances replacing covariances.

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