Theor Appl Genet (1991) 81:166–172

Efficiency of indirect selection at selection equilibrium

B. Villanueva and B. W. Kennedy *

Centre for Genetic Improvement of Livestock, Animal and Poultry Science, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Received July 18, 1990; Accepted July 25, 1990
Communicated by D. Van Vleck

Summary. Efficiency of indirect selection compared with that of direct selection to increase the mean value of some trait has been usually studied by considering a single generation of indirect and direct responses to selection only. However, under continued selection, genetic variances and covariances, and therefore expected genetic responses, change each generation due to linkage disequilibrium. With directional and truncation selection, genetic parameters asymptote to limiting values after several generations. The efficiency of indirect selection is examined in this limiting situation. The ratio of correlated response to direct response for the trait to improve in the limit is compared with the ratio after the first generation of selection. For all initial parameter values for which indirect selection is more efficient than direct selection, relative efficiency of indirect selection is smaller in the limit than in the first generation. For some parameter values, indirect selection is more efficient than direct selection in the first generation, but less efficient in the limit. Expressions for minimum values of the initial genetic correlation and heritability of the alternative trait required for indirect selection to be preferred in the limit are derived. These values are higher when limiting responses are used instead of single generation responses. The loss in relative efficiency of indirect selection from changes in genetic parameters due to selection should be taken into account when applications of indirect selection are considered.

Key words: Indirect selection – Correlated response – Linkage disequilibrium

Introduction

Indirect selection refers to selection on an alternative trait when the goal is to change the mean value of another correlated trait (desired trait). The genetic response in the desired trait is achieved through its genetic correlation with the alternative trait. Situations where indirect selection can be preferable have been discussed by several authors (e.g. Falconer 1981; Searle 1965). Indirect selection is often considered when the desired trait is expensive or difficult to measure.

Searle (1965) discussed conditions under which indirect selection might be preferable to direct selection when mass selection is practised. His conclusions were based on the conventional prediction equations for direct and indirect genetic responses (e.g. Falconer 1981). However, under continued selection these equations overestimate responses because they do not account for reduction of genetic (co)variability (Bulmer 1971; Bulmer 1980). Assuming infinite numbers of loci and population size, change in population genetic variances and covariances when selection is practised is due to the generation of linkage disequilibrium (Bulmer 1980). After a few cycles of directional selection by truncation, genetic parameters asymptote to limiting values and an equilibrium is approached in which the new selection disequilibrium is offset by recombination. With unlinked loci the equilibrium is approached within three to four generations of selection. Expressions for the limiting values of genetic parameters are given by Gomez-Raya and Burnside (1990) and Villanueva and Kennedy (1990a).

Changes in genetic parameters as a consequence of generation of linkage disequilibrium induced by selection were not considered in previous studies of indirect selection. The purpose of this paper is to examine efficiency of indirect selection when equilibrium is approached after repeated cycles of selection.

---

* To whom correspondence should be addressed

Efficiency of indirect selection in the first generation of selection

The model considered is the same as that described in Villanueva and Kennedy (1990a). Briefly, the assumptions were: (1) each trait is controlled by an infinite number of unlinked loci with small effects acting additively; (2) environmental deviations are normally distributed; (3) population is infinitely large; (4) selection is by truncation on phenotype of the individual for the desired trait (in direct selection) or the alternative trait (in indirect selection); (5) selected parents are mated at random; (6) proportion of individuals selected remains the same for each generation; (7) generations are discrete.

A simple method of measuring the efficiency of indirect selection is the ratio of correlated to direct genetic response (Lerner and Cruden 1948). Values greater than one for this ratio indicate that more rapid genetic progress would be achieved from selection on the alternative trait (trait 1) than from direct selection on the desired trait (trait 2). If selection is based on individual phenotypic values, the ratio of responses or relative efficiency of indirect selection (RE) in the first generation of selection is

$$RE_{(1)} = r_{A(0)} \frac{i_{1(0)}}{i_{2(0)}} \sqrt{\frac{h^2_{1(0)}\,\sigma^2_{A_2(0)}}{h^2_{2(0)}\,\sigma^2_{A_2(0)}}} \tag{1}$$

where subscripts in brackets refer to the generation number, h^2_1 and h^2_2 are heritabilities of traits 1 and 2, r_A is the genetic correlation between both traits, $\sigma^2_{A_2}$ is the genetic variance of the desired trait (trait 2) and i_1 and i_2 are the selection intensities practised. If intensity of selection is the same in both procedures, expression (1) simplifies to

$$RE_{(1)} = r_{A(0)} \sqrt{\frac{h^2_{1(0)}}{h^2_{2(0)}}} \tag{2}$$

This expression was utilized by Searle (1965) to evaluate indirect selection.

Efficiency of indirect selection in the limit

Expression (2) is valid only for one generation of selection. Selection produces changes in genetic variances and covariances. On assuming an infinite population and an infinite number of loci, continued truncation selection leads to an equilibrium situation that is approached rapidly if loci are unlinked.

With a constant selection intensity (i_1) across generations, expected correlated response in trait 2 when selection is practised on trait 1 in the limit (subscript L) is

$$CR_{2(L)} = i_1\, h_{1(L)}\, r_{A(L)}\, {}^*\sigma_{A_2(L)}$$

where $h_{1(L)}$ is the limit for the square root of heritability of trait 1, $r_{A(L)}$ is the limit for the genetic correlation and ${}^*\sigma_{A_2(L)}$ is the limit for the genetic standard deviation of trait 2 when selection is on trait 1. Gomez-Raya and Burnside (1990) showed the limit for heritability of the trait under selection is

$$h^2_{1(L)} = \frac{-1+\sqrt{1+4h^2_{1(0)}k_1[1-h^2_{1(0)}]}}{2k_1[1-h^2_{1(0)}]} \tag{3}$$

where k_1 is equal to $i_1\,(i_1 - x_1)$ and x_1 is the standardized deviation of the truncation point from the mean. Villanueva and Kennedy (1990a) showed limits for the genetic correlation ($r_{A(L)}$) and genetic variance of the trait under indirect selection (${}^*\sigma^2_{A_2(L)}$) are

$$r_{A(L)} = \frac{r_{A(0)}}{\sqrt{1+h^2_{1(L)}k_1[1-r^2_{A(0)}]}} \tag{4}$$

and

$${}^*\sigma^2_{A_2(L)} = \frac{\sigma^2_{A_2(0)}}{1+h^2_{1(L)}\,r^2_{A(L)}\,k_1} \tag{5}$$

If a constant selection intensity (i_2) is assumed, expected direct response in the limit when selection is practised on trait 2 is

$$R_{2(L)} = i_2\, h_{2(L)}\, \sigma_{A_2(L)}$$

where $h_{2(L)}$ and $\sigma_{A_2(L)}$ are the limiting values for the square root of the heritability and the genetic standard deviation of trait 2, when trait 2 is directly selected. The limit for the genetic variance of the trait under direct selection is

$$\sigma^2_{A_2(L)} = \frac{\sigma^2_{A_2(0)}}{1+h^2_{2(L)}k_2} \tag{6}$$

(Gomez-Raya and Burnside 1990) where k_2 is $i_2\,(i_2 - x_2)$ and x_2 is the standardized deviation of the truncation point from the mean and $h^2_{2(L)}$ is heritability in the limit of the trait under direct selection:

$$h^2_{2(L)} = \frac{-1+\sqrt{1+4h^2_{2(0)}k_2[1-h^2_{2(0)}]}}{2k_2[1-h^2_{2(0)}]}$$

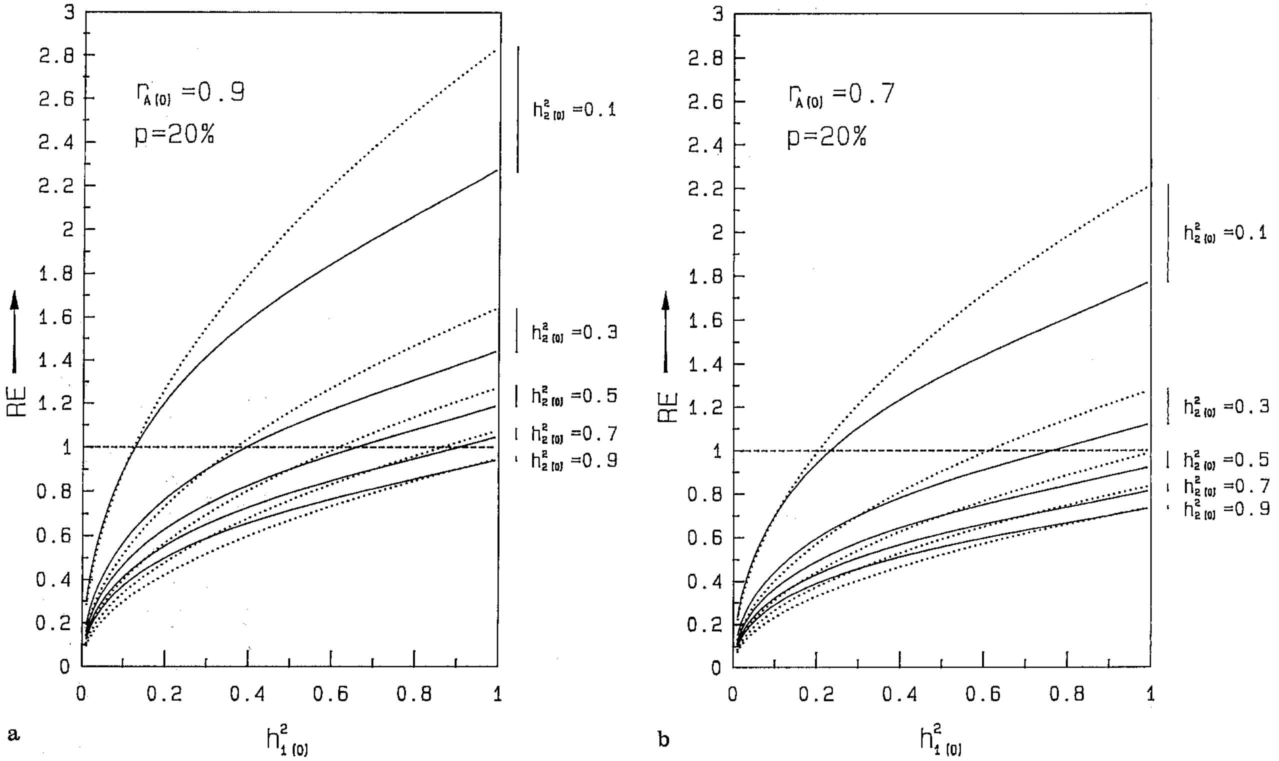
Then, the relative efficiency in the limit ($RE_{(L)}$) is

$$RE_{(L)} = \frac{CR_{2(L)}}{R_{2(L)}} = \frac{i_1\, h_{1(L)}\, r_{A(L)}\, {}^*\sigma_{A_2(L)}}{i_2\, h_{2(L)}\, \sigma_{A_2(L)}}$$

which reduces to

$$RE_{(L)} = r_{A(L)} \sqrt{\frac{h^2_{1(L)}\, {}^*\sigma^2_{A_2(L)}}{h^2_{2(L)}\, \sigma^2_{A_2(L)}}} \tag{7}$$

when selection intensity is the same for both selection procedures.



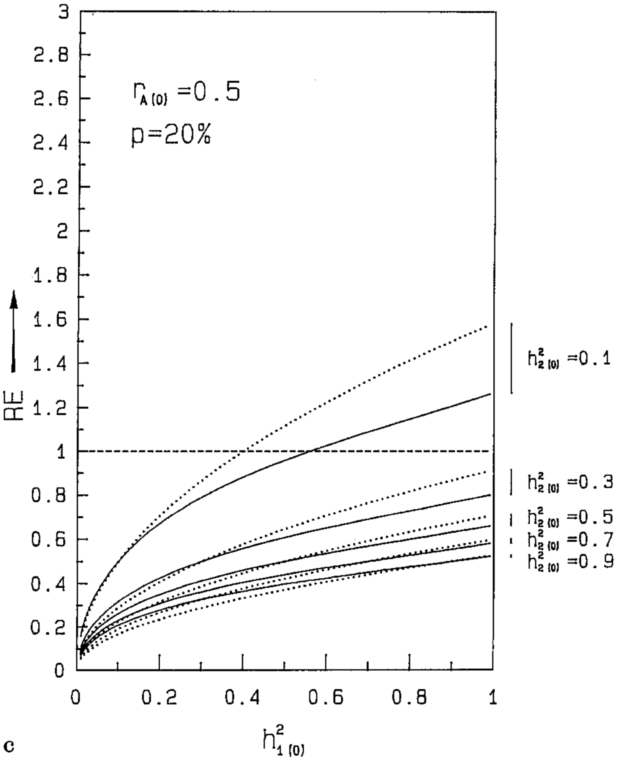


Fig. 1a–c. Efficiency of indirect selection in the first generation of selection (*dotted lines*) and in the limit (*solid lines*) when the proportion selected (p) is 20%

It should be noted that $^*\sigma^2_{A_2(L)} \neq \sigma^2_{A_2(L)}$, and therefore the terms do not cancel as happens if only the first generation of selection is considered. Substituting (5) and (6), eq. (7) becomes

$$RE_{(L)} = r_{A(L)} \sqrt{\frac{h^2_{1(L)}[1+h^2_{2(L)}\,k]}{h^2_{2(L)}[1+h^2_{1(L)}\,r^2_{A(L)}\,k]}} \tag{8}$$

where $k=k_1=k_2$.

Thus RE in the limit depends not only on initial values of genetic correlation and heritabilities in both traits but also on selection intensity practised (limiting values of h^2_1, h^2_2 and r_A depend on initial values and on intensity of selection). Intensity of selection, however, appears to have less influence on the change in heritabilities and genetic correlation than the initial genetic parameters (Gomez-Raya and Burnside 1990; Villanueva and Kennedy 1990a).

Figure 1 shows relative efficiency both in the first generation of selection and in the limit as a function of the initial heritability of trait 1. Five different values of initial heritability of trait 2 were considered (0.1, 0.3, 0.5, 0.7 and 0.9). Selection intensity assumed corresponded to a selected proportion of 20%. Three different values of the genetic correlation in the base population were considered (0.9, 0.7 and 0.5 in Fig. 1 a, b, c, respectively). Indirect selection is more efficient than direct selection for heritabilities above the horizontal dashed line at the ordinate value of 1. If $h^2_{1(0)} = h^2_{2(0)}$, then $h^2_{1(L)} = h^2_{2(L)}$ and $RE_{(L)} = RE_{(1)} = r_{A(0)}$ as can be derived from eq. (8). When $h^2_{1(0)}$ is less than $h^2_{2(0)}$, $RE_{(L)}$ is greater than $RE_{(1)}$. The reverse occurs when $h^2_{1(0)}$ is greater than $h^2_{2(0)}$; in this case $RE_{(L)}$ is always smaller than $RE_{(1)}$. For all cases in which indirect selection results in a greater response than direct selection; i.e., $RE > 1$, values of $RE_{(L)}$ are always smaller than those of $RE_{(1)}$. Differences between $RE_{(L)}$ and $RE_{(1)}$ increase with $r_{A(0)}$. For values of $RE > 1$, these differences decrease with $h^2_{2(0)}$ and increase with $h^2_{1(0)}$. Also, for some combinations of genetic parameters indirect selection is more efficient than direct selection in the first generation, but less efficient in the limit.

Minimum requirements in initial genetic parameters

Minimum values that initial genetic parameters should have for indirect selection to be more efficient than direct selection in the limit will now be considered. As pointed by Searle (1965) there can be situations where, for economic or other reasons, indirect selection is preferred even though RE is less than one. However, in general, indirect selection will be preferred when RE is greater than one; i.e. when a greater rate of genetic improvement is achieved relative to that obtained by direct selection. In the limit, indirect selection will have a higher rate of response than direct selection when $RE_{(L)} > 1$ or

$$r_{A(L)} \sqrt{\frac{h^2_{1(L)}[1 + h^2_{2(L)} k]}{h^2_{2(L)}[1 + h^2_{1(L)} r^2_{A(L)} k]}} > 1$$

Squaring both sides in this inequality and rearranging terms,

$$h^2_{1(L)}\,[1 + h^2_{2(L)} k] > \frac{h^2_{2(L)}[1 + h^2_{1(L)} r^2_{A(L)} k]}{r^2_{A(L)}}$$

and reworking this expression shows that $RE_{(L)}$ is greater than 1 when

$$h^2_{1(L)} > \frac{h^2_{2(L)}}{r^2_{A(L)}} \qquad (9)$$

which is the equivalent expression in the limit to that obtained by Searle (1965) for the first generation of selection. This expression can be used to show (Appendix) that the minimum value of h^2_1 in the base population for indirect selection to be more efficient than direct selection is

$$h^2_{1(0)} > \frac{\gamma\,[1 + \gamma\, k]}{1 + \gamma^2 k}$$

for

$$\gamma = \frac{h^2_{2(L)}}{r^2_{A(0)} - h^2_{2(L)} k [1 - r^2_{A(0)}]}, \qquad 1 > \gamma > 0 .$$

Minimum values of initial heritability of the alternative trait for several combinations of initial values of genetic correlation and heritability of the desired trait are given in Table 1. The minimum value of heritability of the alternative trait depends not only on the genetic correlation and heritability of the desired trait (as when only single generation responses are considered), but also on selection intensity. Two intensities of selection corresponding to selected proportions of 1% and 50% were considered. The minimum value of $h^2_{1(0)}$ required for indirect selection to be preferred increases with selection intensity. Differences between selection intensities (with respect to minimum value of $h^2_{1(0)}$) decreases with $r_{A(0)}$ and increases with $h^2_{2(0)}$. Also, even with the weakest selection considered ($p = 50\%$), minimum values required for $h^2_{1(0)}$ are larger than those obtained by Searle (1965) who considered only the first generation. Only when selection intensity and $h^2_{2(0)}$ are very low and $r_{A(0)}$ is very high is the minimum $h^2_{1(0)}$ required in the limit the same as in the first generation of selection (data not shown). For example, when the selected proportion is 90%, $r_{A(0)}$ is 0.8 and $h^2_{2(0)}$ is 0.1, the minimum value of $h^2_{1(0)}$ in both the first generation and in the limit is 0.16.

Also, (9) can be rearranged as

$$r^2_{A(L)} > \frac{h^2_{2(L)}}{h^2_{1(L)}}$$

and if the value of $r^2_{A(L)}$ in (4) is substituted in this inequality, then the minimum value of $r_{A(0)}$ required for given

Table 1. Minimum heritability of alternative trait for indirect selection to be more efficient than direct selection in the limit when the proportion selected (p) is 1% or 50%

$h^2_{2(0)}$	p (%)	$r_{A(0)}$					
		0.4	0.5	0.6	0.7	0.8	0.9
		Minimum $h^2_{1(0)}$					
0.1	1		0.59	0.36	0.24	0.17	0.13
	50	0.91	0.53	0.33	0.23	0.17	0.13
0.2	1			0.78	0.52	0.36	0.26
	50			0.71	0.48	0.34	0.26
0.3	1				0.79	0.55	0.40
	50				0.74	0.53	0.39
0.4	1					0.73	0.53
	50				0.96	0.70	0.52
0.5	1					0.90	0.67
	50					0.87	0.65
0.6	1						0.79
	50						0.78
0.7	1						0.91
	50						0.90

Table 2. Minimum genetic correlation for indirect selection to be more efficient than direct selection in the limit when the proportion selected (p) is 1% or 50%

$h^2_{2(0)}$	p (%)	$h^2_{1(0)}$								
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
		Minimum $r_{A(0)}$								
0.1	1	1.00	0.75	0.64	0.57	0.53	0.50	0.50	0.44	0.42
	50	1.00	0.74	0.62	0.56	0.51	0.47	0.45	0.42	0.40
0.2	1		1.00	0.85	0.77	0.71	0.66	0.63	0.59	0.57
	50		1.00	0.85	0.75	0.69	0.64	0.60	0.57	0.54
0.3	1			1.00	0.90	0.83	0.77	0.73	0.70	0.66
	50			1.00	0.89	0.82	0.76	0.71	0.68	0.64
0.4	1				1.00	0.92	0.86	0.81	0.77	0.74
	50				1.00	0.92	0.85	0.80	0.76	0.72
0.5	1					1.00	0.94	0.88	0.84	0.80
	50					1.00	0.93	0.88	0.83	0.79
0.6	1						1.00	0.94	0.90	0.85
	50						1.00	0.94	0.89	0.85
0.7	1							1.00	0.95	0.90
	50							1.00	0.95	0.90
0.8	1								1.00	0.95
	50								1.00	0.95
0.9	1									1.00
	50									1.00

values of $h^2_{1(0)}$ and $h^2_{2(0)}$ is obtained as

$$r_{A(0)} > \sqrt{\frac{h^2_{2(L)}[1+h^2_{1(L)}k]}{h^2_{1(L)}[1+h^2_{2(L)}k]}}$$

Minimum values required for initial genetic correlation for several values of $h^2_{1(0)}$ and $h^2_{2(0)}$ are given in Table 2. The same selection intensities as in Table 1 were considered. As expected, minimum $r_{A(0)}$ required increases with heritability of the desired trait and decreases with heritability of the alternative trait. Minimum $r_{A(0)}$ required increases with intensity of selection. Differences in minimum values of $r_{A(0)}$ with respect to the two selection intensities considered are greatest when $h^2_{2(0)}$ is low, but even then differences are very small. The effect of selection intensity is not very important. The minimum genetic correlation not only depends on heritability of the desired trait (as when only the first generation of selection is considered), but also on heritability of the alternative trait and on selection intensity. Even with the relatively weak selection intensity associated with 50% selected (requirements are smaller than for 1% selected), the smallest number for a given $h^2_{2(0)}$ (that corresponding to the largest $h^2_{1(0)}$) is greater than the corresponding value obtained by Searle (1965). For example, if $h^2_{2(0)}=0.3$, the smaller $r_{A(0)}$ required is that corresponding to $h^2_{1(0)}=0.9$. This value is 0.64 which is greater than the 0.55 obtained by Searle (1965). Even with selection intensity as slight as that corresponding to a selected proportion of 90%, the minimum $r_{A(0)}$ required for indirect selection to be preferred in the limit is higher than the minimum value required when only the first generation of selection is considered.

Discussion

In general, larger rates of genetic improvement are expected with indirect selection when heritability of the alternative trait is substantially higher than heritability of the desired trait and the genetic correlation between both traits is high (Searle 1965). However, if heritability of the alternative trait is larger than heritability of the desired trait, then relative efficiency of indirect selection in the limit is always smaller than in the first generation of selection. Also, this difference increases with the genetic correlation and with the heritability of the alternative trait and decreases with the heritability of the desired trait. Therefore, in all the cases in which indirect selection can be expected to be superior to direct selection, the relative efficiency has been overestimated in previous studies because the change in genetic parameters due to linkage disequilibrium generated by selection was ignored.

Wray and Hill (1989) have compared different breeding programmes by using expected responses in the limit. Although the relative efficiencies of the different schemes changed in the limit with respect to the first generation, they concluded that the same selection programme would be likely to be chosen no matter which kind of predictions were used. In general, our results agree with this. However, in some cases, indirect selection would give a larger rate of response than direct selection in the first generation, but a smaller rate in the limit (Fig. 1). Thus, loss in efficiency of indirect selection may even lead to a change in the ranking of the two selection methods.

Another way to examine reduction in relative efficiency of indirect selection is by looking at the minimum initial values that heritability of the alternative trait and the genetic correlation between the two traits should have for indirect selection to be preferred after repeated cycles of selection. When expected responses in the limit are considered, these values are greater than those obtained by Searle (1965), who considered only first generation responses. Thus, minimum requirements in heritability of the alternative trait and genetic correlation between the traits for preference for indirect selection are greater after several generations of selection.

The criterion used to evaluate efficiency of indirect selection was the ratio CR_2/R_2. This criterion does not account for economic aspects. In some cases the ratio can be smaller than one, and still indirect selection can be preferred to direct selection if the desired trait is very expensive to measure.

Rate of response for the desired trait can be increased by combined selection, i.e. combining desired and alternative traits in a selection index (Searle 1965; Walkley and Smith 1980; Woolliams and Smith 1988). However, this procedure can not be used in many cases where indirect selection can be applied. An example is selection for some trait in one environment when improvement of the same trait in a different environment is desired. The problem of genotype by environment interaction can be studied following the approach of Falconer (1952) by considering performance in different environments as different correlated traits. This can be considered as a case of indirect selection that does not allow combined selection. Another example is when selection is based on partial lactation records where the true objective is to increase total yield in dairy cattle. Similar considerations apply to the selection of young animals at an early age on the basis of physiological markers of genetic merit for a performance trait. In all these cases use of traditional formulae will overestimate indirect response.

Two assumptions in this study were that the population is of infinite size and that generations do not overlap. Relaxations of these assumptions have been discussed by Wray and Hill (1989). Random fluctuations due to genetic drift in finite populations will lead to further changes in genetic parameters. However these changes will be more important in later generations of selection as inbreeding accumulates. Changes by linkage disequilibrium considered in this work occur mostly in the early generations. On the other hand, discrete generations were assumed for simplicity. Overlapping generations would reach the same end. Also, throughout this study initial genetic parameters have been assumed to be known without error. In practice, estimation of these parameters is necessary. Some concerns in applying indirect selection in practice relate to errors in the estimation of parameters (e.g. Walkley and Smith 1980). Large standard errors in estimating RE make indirect selection less valuable (Searle 1965). Also, efficiency of indirect selection can be seriously reduced when the assumption of a infinite number of loci is relaxed (Villanueva and Kennedy 1990b). All of these considerations result in the response to indirect selection being less efficient than expected from the simple prediction formulae usually used. Such simple predictions are overly optimistic. These concerns need to be recognized in deciding whether or not to apply indirect selection in practical breeding programmes.

Acknowledgements. We wish to thank Dr. C. Smith and L. Gomez-Raya for their useful comments. This study was supported by a grant from the Instituto Nacional de Investigaciones Agrarias, Spain.

Appendix

By substituting (4) in (9), some algebra shows the following inequality:

$$h^2_{1(L)}\,[r^2_{A(0)} - h^2_{2(L)}\,k(1 - r^2_{A(0)})] > h^2_{2(L)}\ .$$

Then,

$$h^2_{1(L)} > \frac{h^2_{2(L)}}{r^2_{A(0)} - h^2_{2(L)}\,k[1 - r^2_{A(0)}]} \quad \text{if} \quad r^2_{A(0)} - h^2_{2(L)}\,k[1 - r^2_{A(0)}] > 0$$

and

$$h^2_{1(L)} < \frac{h^2_{2(L)}}{r^2_{A(0)} - h^2_{2(L)}\,k[1 - r^2_{A(0)}]} \quad \text{if} \quad r^2_{A(0)} - h^2_{2(L)}\,k[1 - r^2_{A(0)}] < 0\ .$$

However, the latter case is not possible because both $h^2_{2(L)}$ and $h^2_{1(L)}$ are always non-negative.

$$\text{Let} \quad \gamma = \frac{h^2_{2(L)}}{r^2_{A(0)} - h^2_{2(L)}\,k[1 - r^2_{A(0)}]} \quad \text{for} \quad 1 > \gamma > 0\ .$$

Then $h^2_{1(L)} > \gamma$ and substituting $h^2_{1(L)}$ for its value given in (3),

$$\frac{-1 + \sqrt{1 + 4h^2_{1(0)}\,k[1 - h^2_{1(0)}]}}{2k[1 - h^2_{1(0)}]} > \gamma$$

or

$$\sqrt{1 + 4h^2_{1(0)}\,k[1 - h^2_{1(0)}]} > 2\gamma k[1 - h^2_{1(0)}] + 1\ .$$

Squaring both sides in this inequality gives

$$1 + 4h^2_{1(0)}\,k[1 - h^2_{1(0)}] > [2\gamma k[1 - h^2_{1(0)}] + 1]^2$$

and reworking this expression gives

$$-[1 + \gamma^2 k]\,h^4_{1(0)} + [1 + 2\gamma^2 k + \gamma]\,h^2_{1(0)} - \gamma\,[1 + \gamma k] > 0 \qquad (\mathrm{A}\,1)$$

Solving for $h^2_{1(0)}$, the two roots of this second degree equation are $\frac{\gamma\,[1 + \gamma k]}{1 + \gamma^2 k}$ and 1. Therefore (A 1) can be rewritten as

$$\left[h^2_{1(0)} - \frac{\gamma\,[1 + \gamma k]}{1 + \gamma^2 k}\right][1 - h^2_{1(0)}] > 0$$

Because $[1 - h^2_{1(0)}]$ is greater than (or equal to) zero, $\left[h^2_{1(0)} - \frac{\gamma\,[1 + \gamma k]}{1 + \gamma^2 k}\right]$ has to be positive. Thus, the minimum value of the initial heritability of the alternative trait for indirect selection to be more efficient than direct selection in the limit is

$$h^2_{1(0)} > \frac{\gamma\,[1 + \gamma k]}{1 + \gamma^2 k}\ .$$

References

Bulmer MG (1971) The effect of selection on genetic variability. Am Nat 105:201–211

Bulmer MG (1980) The mathematical theory of quantitative genetics. Clarendon Press, Oxford

Falconer DS (1952) The problem of environment and selection. Am Nat 86:293–298

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, New York

Gomez-Raya L, Burnside EB (1990) The effect of repeated cycles of selection on genetic variance, heritability, and response. Theor Appl Genet 79:568–574

Lerner IM, Cruden DM (1948) The heritability of accumulative monthly and annual egg production. Poultry Sci 27:67–77

Searle SR (1965) The value of indirect selection: I. Mass selection. Biometrics 21:682–707

Villanueva B, Kennedy BW (1990 a) Effect of selection on genetic parameters of correlated traits. Theor Appl Genet (in press)

Villanueva B, Kennedy BW (1990 b) Efficiency of indirect selection with a finite number of loci. In: Proc 4th World Congr Genet Appl Livest Prod, Edinburgh Vol XIII:265–268

Walkley JRW, Smith C (1980) The use of physiological traits in genetic selection for litter size in sheep. J Reprod Fert 59:83–88

Woolliams JA, Smith C (1988) The value of indicator traits in the genetic improvement of dairy cattle. Anim Prod 46:333–345

Wray NR, Hill WG (1989) Asymptotic rates of response from index selection. Anim Prod 49:217–227