Indirect selection criteria against clean wool colour in Corriedale sheep and their effects on wool production traits

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Abstract

The potential of greasy wool colour subjective assessment Visual Colour Score (VCS) and the yellow predictive test (YPC) as indirect selection criteria for reduction of clean wool colour (CWC) in Corriedale sheep was examined. The heritability of these wool colour traits and the wool production traits, greasy (GFW) and clean fleece weights (CFW), and mean fibre diameter (MFD) and the phenotypic and genetic correlations among these traits were estimated from a Corriedale flock using AIREML procedures. A high genetic correlation between YPC and CWC was observed, indicating that YPC could be a suitable indirect selection criterium for CWC. However, direct selection against CWC was predicted to produce faster genetic improvements in CWC than that expected under indirect selection via YPC. Single trait selection based on VCS or YPC were expected to reduce the response in CWC to 51% and 49% of that estimated for direct selection. The positive genetic correlations of CWC, YPC and VCS with CFW and MFD would cause a reduction in both MFD and CFW to result from selection that reduces wool colour. The results showed that the most effective way to genetically improve CWC was through indirect selection to reduce MFD, CFW or GFW, followed by direct selection, but the premiums for CWC in the Corriedale breed may not be sufficient to justify the expected losses in CFW.

Key words: wool yellowing susceptibility, genetic parameter estimates, selection responses.

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Introduction

Reductions in clean wool colour are sought by wool breeders because yellow wool is penalised in price due to a loss in versatility in dyeing. Studies on the genetics of wool yellowing have found that the heritability of clean wool colour (CWC) - measured in Y-Z units - varies from 0.04 ± 0.07 in Romney sheep in New Zealand (Hawker et al., 1988) to 0.42 ± 0.14 for Collinsville Merinos in Australia (James et al., 1990). The variation between these heritability estimates might have been due to environmental variation caused by differences in weather conditions between the locations of these studies. The incidence of yellow wool is notably higher in warmer and wetter weather conditions. Consequently, selection based on scoured wool colour is likely to be ineffective since the trait is unlikely to be adequately expressed in all locations in all years. The finding of a suitable indirect selection criterion may be a better approach to selection against wool yellowing in low rainfall areas.

The potential for selection of wool colour traits, namely visual colour score of greasy (VCS) wool and yel-

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low predictive colour (YPC) as indirect selection criteria against CWC, were investigated. The YPC technique was developed by Wilkinson (1981), and is based on the incubation of wool samples at warm temperature and high humidity. The technique mimics the environmental conditions favourable for wool yellowing. The resulting YPC score should equate to the level of wool yellowing found under highly challenging weather conditions. Yellow predictive colour has previously been studied as an indicator of the susceptibility of sheep to wool yellowing (Wilkinson, 1981) and fleece rot (Cottle, 1996).

The objectives of the current experiment were to establish the genetic correlation between CWC and YPC to evaluate YPC as indirect selection criterium against clean wool colour and to estimate the correlated responses in other wool production traits.

Material and methods

Animals

Data were collected from the Corriedale sire progeny test flock (Sheep Breeding Unit, Lincoln University, Canterbury) described in Benavides *et al.* (1998). A total of 440

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contemporary progeny from 19 sires and 253 dams were tested, with an average of 22 offspring per sire. Sire selection was based on superiority in greasy fleece weight (GFW) and/or liveweight. Each sire was mated to 25 randomly allocated ewes.

All lambs were first shorn in January, at approximately 18 weeks of age. Greasy fleece weight, clean fleece weight (CFW) and Yield were determined at shearing in August and in October of each year for ram and ewe hoggets, respectively. However, mean fibre diameter (MFD), CWC, YPC and VCS were determined from midside samples taken in August from both sexes in each year in accordance with AS/NZS (1999a).

Clean wool colour was measured in Y-Z units on scoured samples after the wool tips and any vegetable matter had been removed. Samples were cut into 20 mm lengths and air-blended. Clean wool colour was measured, recording the X, Y, and Z tristimulus values using a Hunterlab D25 colorimeter with the illuminant 2/10° (New Zealand Standards, 1984).

Clean fleece weight was obtained from measurements of scoured yield and GFW according to the Australian/New Zealand Draft Standard for flock testing (AS/NZS 1999b). The samples were scoured, dried at 60 °C for 20 min, and then conditioned for 12 h at 20 ± 2 °C and 65 $\pm 2\%$ relative humidity to calculate scoured yield. Clean sample weight was recorded at 16% regain for scoured yield calculations. Clean fleece weight was calculated from GFW based on scoured yield at 16% regain.

Mean fibre diameter was measured by Optical Fibre Diameter Analyser (AS/NZS, 1999c) (International Wool Textile Organisation, 1995). Visual greasy wool colour score (VCS) was subjectively assessed and scored from 1 to 10, score 1 being white wool and 10 being intense yellow discoloured. Wool yellowing susceptibility was determined using the YPC technique described by Raadsma and Wilkinson (1990).

Statistical analysis

Data were analysed using the General Linear Model (GLM) procedure of SAS V6 (SAS/STAT, 1990) to determine significant effects. Year of birth, sex, age of dam, birth and rearing ranks were fitted as fixed effects. Date of birth was fitted as a covariate and sire within year was included as a random effect.

The model fitted to each variable was:

$$Y_{ijklmno} = \mu + y_i + x_j + a_k + br_l + rr_m + dob_{ijklmno} + s_n(y_i) + e_{ijklmno}$$

where $Y_{ijklmno}$ was the record of the oth individual; μ was the population mean; y_i was the year of birth; x_j was the sex; a_k was the age of dam; br_i was the birth rank, rr_m was the rearing rank; $dob_{ijklmno}$ was the date of birth; $s_n(y_i)$ was the sire within year of birth, and $e_{ijklmno}$ was the residual error.

For GFW, CFW and Yield traits, sex was confounded with time of sampling. Interactions between fixed effects were initially fitted in the model. Non significant interactions and effects (p \geq 0.05) were removed from the final analysis. Estimates of heritability and genetic and phenotypic correlations were calculated using the animal model of the Average Information Restricted Maximum Likelihood programme (AIREML) (Johnson and Thompson, 1995).

Restricted selection indices were calculated using the SELIND2 programme (Cunningham and Mahon, 1977) based on combined heritability, phenotypic and genetic correlation estimates of the traits studied. The relative economic values (REV) for the breeding objective traits were calculated by regression analyses from Wools of New Zealand wool prices data for the three wool selling seasons 96/97-98/99. The regression equations of price on MFD and CWC were: $NZ\phi = 765 - 7.99$ MFD and $NZ\phi = 550 -$ 10.3 Y-Z respectively (both p < 0.05) giving REV of NZ\$ -0.08/µm kg clean and NZ\$ -0.10/Y-Z kg clean respectively. The REV of CFW for Corriedale wool was NZ\$ +5.38/kg (Wools of New Zealand: R. Munson, pers. comm.). All direct and correlated responses in this study were expressed in units per individual per year based on calculations assuming selection of 1% of rams and 40% of ewes, with an average generation interval of 3.12 years.

Results

Among the environmental effects fitted in the model, year of birth significantly affected (p < 0.05) all traits studied except MFD. Visual colour score, CWC, CFW and MFD were significantly affected by sex. Birth and rearing ranks did not affect any of the traits (p \geq 0.05) but age of dam affected GFW (p < 0.05).

Yellow predictive colour and VCS frequencies are presented in Table I. Heritability estimates, phenotypic and genetic correlations for all traits studied are summarised in Table II. Standard errors were generally high, possibly due in part to the small size of the dataset used.

Table I - Frequency of Yellow predictive colour (YPC) and Visual colour score (VCS) scores for the Corriedale population studied.

Score frequencies (%)	1	2	3	4	5	6	7	8	9	10
YPC	0	0	0	0.5	3.9	23.0	33.9	29.4	7.5	1.8
Visual score	0	0	0.5	2.6	8.5	16.1	29.9	30.6	9.0	2.8

Table II - Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations (± standard error) between wool production traits and wool colour traits analysed in Corriedale flock.

	GFW (kg)	CFW (kg)	MFD (μm)	YPC (score)	VCS (score)	CWC (Y-Z units)
σ^{2}_{P}	(0.29)	(0.16)	(6.67)	(1.13)	(1.30)	(0.66)
GFW	0.52 ± 0.15	0.89 ± 0.05	0.58 ± 0.16	0.65 ± 0.26	0.72 ± 0.16	0.44 ± 0.31
CFW	0.92 ± 0.01	$\textbf{0.37} \pm \textbf{0.15}$	0.79 ± 0.14	0.57 ± 0.31	0.67 ± 0.20	0.91 ± 0.24
MFD	0.46 ± 0.05	0.50 ± 0.04	$\textbf{0.65} \pm \textbf{0.15}$	0.23 ± 0.29	0.29 ± 0.22	0.93 ± 0.18
YPC	0.17 ± 0.05	0.09 ± 0.05	0.07 ± 0.05	$\textbf{0.16} \pm \textbf{0.10}$	0.99 ± 0.12	0.64 ± 0.31
VCS	0.35 ± 0.05	0.21 ± 0.06	0.22 ± 0.06	0.54 ± 0.04	$\textbf{0.44} \pm \textbf{0.14}$	0.40 ± 0.28
CWC	0.13 ± 0.05	0.16 ± 0.05	0.26 ± 0.05	0.20 ± 0.05	0.21 ± 0.05	$\boldsymbol{0.27 \pm 0.13}$

GFW = greasy fleece weight; CFW = clean fleece weight; MFD = mean fibre diameter; YPC = yellow predictive colour; VCS = visual colour score; CWC = clean wool colour.

Phenotypic correlations of CWC and YPC with wool production traits were all of low magnitude (0.07-0.26). The phenotypic correlation estimates between Visual score and wool production traits were also low except for that with GFW (0.35 \pm 0.05).

The estimates of heritability of YPC and CWC were 0.16 ± 0.10 and 0.27 ± 0.13 , respectively (Table II). The heritability for Visual score, GFW, CFW and MFD were estimated at 0.44 ± 0.14 , 0.52 ± 0.15 , 0.37 ± 0.15 and 0.65 ± 0.15 , respectively.

The genetic correlation estimates for CWC with YPC and VCS were 0.64 ± 0.31 and 0.40 ± 0.28 , respectively. Genetic associations of CWC with wool production traits were moderate, except for the strong positive correlations with CFW and MFD of 0.91 ± 0.24 and 0.93 ± 0.18 respectively (Table II).

The genetic correlation estimates of YPC with fleece weights (GFW and CFW) were 0.65 ± 0.26 and 0.57 ± 0.31 , respectively, while the estimate with MFD was of low magnitude and did not differ significantly from zero (Table II). Genetic correlations of VCS with both GFW and CFW

were higher than those observed between YPC and these fleece weight traits.

Results indicated that a genetic improvement of -0.13 Y-Z/head/year (hereafter Y-Z/year) would be expected from direct selection against CWC. The results also showed that responses on CWC through indirect selection against Visual colour score and YPC would be 51% and 49%, respectively, that of the expected gains from single trait selection against CWC (Table III). The expected changes in the breeding objective traits for wool (CWC, CFW and MFD) after single selection against each of the traits studied are shown in Table IV. These results show that indirect selection against MFD would cause the greatest improvement in CWC, even higher than that expected for direct selection against CWC.

Three indices were derived using the parameters from Table II for a breeding objective to optimise the combined financial gain in CFW, MFD and CWC (Table V). For example, the selection index having CFW, MFD and CWC as the selection criteria traits, was derived as Index 1 (I_1): I_1 = + 1.15CFW + 0.13MFD + 0.43CWC. Expected correlated

Table III - Per annum expected correlated responses on clean wool colour (CWC) based on indirect single trait selection on colour and wool production traits. Correlated responses in units of standardised selection differential per generation are in square brackets.

			Predicted genetic gains o	n clean wool colour/hd/year	Relatives
Trait	h^2	r _{G CWC.ind}	Direct selection ²	Correlated responses ³	genetic potential (RGP) ⁴
Direct selection against CWC:					
Clean wool colour (Y-Z)	0.27		-0.13 (-0.22)		100
Direct selection against:					
YPC (score)	0.16	0.64		-0.06 (-0.11)	+49
VCS score	0.44	0.40		-0.07 (-0.11)	+51
GFW (kg)	0.52	0.44		-0.08 (-0.13)	+61
CFW (kg)	0.37	0.91		-0.14 (-0.23)	+107
MFD (µm)	0.65	0.93		-0.18 (-0.32)	+144

²Direct response = $i * h_X^2 * \sigma_{PX}$ (Falconer, 1989). Proportion of selected sires and dams have been fixed at 1% and 40%, respectively.

 $^{{}^{3}}CR_{Y} = i * h_{X} * h_{Y} * r_{GXY} * \sigma_{PY}$ (Falconer, 1989).

 $^{{}^{4}}RGP = (DR_{ind}/DR_{CWC})*100 \text{ (Raadsma et al., 1987)}.$

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Fable IV - Expected annual correlated responses from direct downward single trait selection of either clean wool colour, YPC or Visual on CFW, MFD and clean wool colour (CWC) and economic return. Correlated responses in units of standardised selection differential per generation are in square brackets.

						Trait selection	lection					
Correlated trait	CFW (kg/hd/yr)	CFW Gain (kg/hd/yr)	CFW (kg/hd/yr)	Gain (NZ\$hd/yr)	MFD (µm/hd/yr)	Gain (NZ\$/hd/yr)	CWC (Y-Z/hd/yr)	CWC Gain (Y-Z/hd/yr) (NZ\$/hd/yr)	YPC (Score/hd/yr)	YPC Gain (Score/hd/yr)	VCS Gain (Score/hd/yr) (NZ\$/hd/yr)	Gain (NZ\$/hd/yr)
CFW	-0.09 (-0.15)	-0.48	-0.09 (-0.15)	-0.48	-0.09 (-0.15)	-0.48	-0.07 (-0.12)	-0.38	-0.03 (-0.05)	-0.16	-0.06	-0.32
MFD	-0.51 (-0.88)	+0.04	-0.59 (-1.01)	+0.05	-0.97 (-1.66)	+0.08	-0.58 (-0.97)	+0.05	-0.15^{1} (-0.25)	+0.01	-0.24 (-0.41)	+0.02
CWC	-0.08 (-0.14)	+0.01	-0.13 (-0.23)	+0.01	-0.18 (-0.31)	+0.02	-0.13 (-0.22)	+0.01	-0.06	+0.01	-0.07 (-0.12)	+0.01
Combined response (CFW + MFD + CWC)		-0.44		-0.42		-0.38		-0.32		-0.14		-0.29

Genetic correlation non significantly different from zero.

responses in each of CFW, MFD and CWC to selection, and the combined annual economic response resulting from changes in these traits, for each of these selection indices, are presented in Table V.

Discussion

The effect of climatic conditions on clean wool colour, here expressed as year of birth, is well documented (Serra and de Matos, 1951; Fraser and Mulcock, 1956; Hoare, 1978). In this study, this trait ranged from -1.37 Y-Z to 2.98 Y-Z for the 1992 progeny measured in 1993 and from -0.24 Y-Z to 6.66 Y-Z for the 1993 progeny measured in 1994, indicating that the latter progeny underwent a greater environmental challenge for the development of wool yellowing. According to Wilkinson's (1981) classification, all individuals with YPC scores ≥ 4 should be considered susceptible to wool yellowing, having the potential to develop detectable levels of non-scourable discolouration. Similarly, animals with YPC scores ≥ 6 should be considered highly susceptible to wool yellowing. Ninetysix percent of the experimental animals in the current study came into this latter category (Table 1). Despite an apparently high level of susceptibility in this flock based on YPC values, the mean clean wool colour, 0.83 ± 0.81 , would be considered white (Wools of New Zealand, 1995). This indicates that the sheep studied were subjected to a low level of natural environmental challenge for wool yellowing.

Information about environmental factors that influence YPC are restricted to observations in Merinos made by Raadsma and Wilkinson (1990) who found that YPC was significantly affected by year. Yellow predictive colour has been found to be strongly phenotypically correlated with suint percentage (Aitken *et al.*, 1994) which can be washed out by rain (Daly and Carter, 1956; Thornberry *et al.*, 1980; Raadsma and Thornberry, 1988). Gender did not affect YPC.

It was also observed that there was no significant $(p \ge 0.05)$ year effect for MFD. Nutritional effects are well known to affect wool fibre diameter (Stewart *et al.*, 1961; Sumner and Wickham, 1969). The fact that year did not affect MFD would indicate that the nutritional levels between years were similar. Unfortunately, there was no measurement of pasture availability during this trial that could support this assertion.

Summarising, it was found that year and sex effects were the main causes for variation in the traits studied. Birth and rearing ranks did not significantly affect any of the traits studied and dam age only differed for GFW. The effect of year was significant for all traits. The levels of clean wool colour over the observed years indicated that fleeces from 1993 were less environmentally challenged than in 1994.

The poor phenotypic correlation between VCS and CWC (0.21 \pm 0.05; Table II) has been discussed in Bena-

Table V - Selection index coefficients (I ₁ to I ₃) and expected annual per head correlated responses in CFW, MFD and clean wool colour (CWC).
Correlated responses in units of standardised selection differential per generation are in square brackets.

			In	dex		
Trait	1	\mathbf{I}_1		I_2		I_3
	Index coefficient	CR	Index coefficient	CR	Index coefficient	CR
CFW	+1.15	+0.11 kg (+0.19)	+1.16	+0.10 kg (+0.18)	+1.15	+0.11 kg (+0.19)
MFD	+0.13	+0.95 µm (+1.63)	+0.16	+0.87 µm (+1.50)	+0.13	+0.79 µm (+1.37)
CWC	+0.43	+0.20 kg (+0.34)	-	+0.19 kg (+0.32)	-	+0.17 kg (+0.30)
YPC	-	-	+0.16	-	-	-
VCS	-	-	-	-	+0.33	-
Combined response (CFW + MFD + CWC)		+ NZ\$0.50		+ NZ\$0.45		+ NZ\$0.51

CR: Correlated response.

vides and Maher (2000). Yellow predictive colour and VCS also had low phenotypically correlated with CWC, indicating that neither VCS nor YPC were accurate predictors of the level of non-scourable discolouration present in fleeces.

The quantification of phenotypic and genetic correlations between YPC and CWC were important objectives of this experiment. Previously, phenotypic studies have only considered small groups of sheep representing extremes of the YPC range, *i.e.* resistant *vs.* susceptible (Wilkinson, 1982; Wilkinson and Aitken, 1985; Aitken *et al.*, 1994). These authors suggested the use of YPC as an indirect selection trait to reduce non-scourable discolouration, despite providing no evidence of a genetic or phenotypic association between these traits. Although these studies showed that extremely "resistant" and "susceptible" groups of sheep produced CWC averages of 1.2 Y-Z and 4.1 Y-Z, respectively (Wilkinson, 1982), the genetic association between YPC and CWC has not previously been demonstrated.

Genetic estimates in this current study were calculated based on a small number of elite sires which may have inflated the genetic variances and co-variances, and these results need to be considered cautiously. The high genetic correlation observed between YPC and CWC (0.64 ± 0.31) in the current study is of importance because it indicates that YPC could be a useful indirect selection criterion for CWC. However, the use of YPC as a selection criterion would only improve CWC by 49% of that obtainable through direct selection on CWC. This occurred because YPC had a low heritability estimate (0.16 \pm 0.10; Table II). Consequently, direct selection against CWC, with a heritability of 0.27 ± 0.13 , would lead to a greater improvement in CWC than selection based on YPC. The heritability for YPC has been estimated at 0.27 ± 0.06 in a larger Corriedale dataset (Benavides et al., 1998). The larger data size is reflected in the lower standard error for this estimate compared with that obtained in this study but the heritability estimate was unaffected.

The use of YPC as an indirect selection criterion for CWC, although resulting in half of the expected genetic gain in CWC (-0.06 Y-Z/year vs. -0.13 Y-Z/year; Table IV), would also halve the estimated reductions in CFW that would occur under selection against CWC colour (-0.03 kg/year vs. -0.07kg/year; Table 4). In economic terms, selection against YPC would result in a loss of NZ\$0.14/year from wool income, being less disadvantageous than the economic losses expected from selection against CWC. However, the expected change in CFW relative to CWC would be similar over any given period for either trait selected. Regardless of whether YPC or CWC is selected against, correlated reductions in CFW appear to be inevitable. Clean fleece weight had the highest relative economic value of the traits considered for Corriedale flocks. Consequently, selection that reduces CWC will reduce the economic gains that would otherwise be possible from increased CFW.

Visual colour score was found to be highly genetically correlated with YPC (0.99 \pm 0.12), therefore, selection against subjective greasy colour assessment (VCS) would reduce susceptibility to wool yellowing. However, the genetic correlation between VCS and CWC (0.40 ± 0.28) was found to be lower than that between YPC and CWC (0.64 \pm 0.51). Visual colour score and YPC may be considered as subjective assessments of the amount of yolk pigments contained in the suint fraction at different stages of environmental challenge. Yellow predictive colour could be argued to be the upper limit of VCS, since YPC is the assessment of the amount of yolk pigments in the greasy wool after incubation. Considering these definitions, CWC appeared to be more genetically correlated to the amount of pigment in suint after incubation. In spite of the lower correlation with CWC, VCS was a slightly better indirect selection criterion against CWC than YPC because it had a higher heritability than YPC.

The positive genetic correlations observed for any of CWC, YPC or VCS with CFW (0.91 \pm 0.24, 0.57 \pm 0.31 and 0.67 \pm 0.20, respectively) would lead to economic

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losses to production under selection to reduce colour in wool since CFW, which is by far the most economically important Corriedale wool trait, would decline. Similar results were found in Romneys (Hawker et al., 1988), where a high genetic correlation between GFW and CWC was realised (0.65 \pm n.a.). Bigham et al. (1983) also estimated that selection against CWC would lead to correlated responses of -0.07 kg GFW and -0.04 kg CFW per generation in Romneys if a proportion of 5% of the population was selected. Surprisingly, Barlow (1974) and Wuliji et al. (1993) reported no significant differences in CWC in progeny of high fleece weight selected Peppin Merino and Romney ewes, respectively, and random control flocks. On the other hand, a negative genetic correlation between CFW and CWC found in Collinsville Merinos (James et al., 1990) indicated that CWC would improve under selection for higher CFW.

The positive genetic correlation estimates between YPC and fleece weights found here also disagree with the findings of Wilkinson and Aitken (1985) who reported negative genetic correlations for YPC with GFW and CFW of -0.41 ± 0.35 and -0.71 ± 0.35 , respectively. These findings suggested that economic gains would result from selection against YPC. Higher genetic correlations between YPC and wool production traits, were observed in the current study than by Raadsma and Wilkinson (1990) and Benavides *et al.* (1998) except for MFD, for which they reported estimates of 0.26 and 0.24 ± 0.14 , respectively.

To avoid the antagonistic economic response between CWC and CFW, an indirect selection trait which has moderate to strong genetic correlations with CWC and CFW of opposing signs would be ideal. Unfortunately, neither YPC nor VCS was found to fulfil these criteria. These results indicate that the genetic origins of yellow discolouration cannot easily be separated from those that determine fleece weight by conventional quantitative genetics.

The use of selection indices to optimise response in a breeding objective containing CFW, MFD and CWC, by using either CWC, YPC or VCS as selection criteria in addition to CFW and MFD showed positive genetic gains for all traits in the objective. Despite the predicted positive overall economic responses from index selection, the major drawback to using these selection indices would be the genetic increase in CWC.

Both Yellow predictive colour and Visual colour score were found to have the potential for indirect selection against CWC. However, both of these traits would give lower correlated responses in CWC higher than that obtained under direct selection. Additionally, YPC and VCS were both positively genetically correlated with CFW, and therefore under single trait selection would also result in net economic losses.

In summary, wool colour traits were predicted to give up to only 51% of the genetic gain in CWC expected under direct selection. MFD had a greater genetic potential to reduce CWC than any other single indirect trait selection. Selection on MFD may be a cost effective means of reducing CWC, since MFD is usually measured for selection purposes for its own importance and no additional cost in wool measurement would be necessary. Despite the steady genetic progress that could be obtained through direct and indirect selection against CWC, such selection would not be economically viable at current wool prices and premiums because of the correlated reductions in CFW that would occur.

Conclusions

Yellow predictive colour and visual colour score can be used as indirect selection criteria to improve clean wool colour. The best indirect selection criteria against CWC was found to be MFD. The fastest genetic progress for CWC would be expected under direct selection. Direct and indirect single trait selection against CWC would be expected to reduce both CFW and MFD. The addition of CWC to an economically weighted index with CFW and MFD would, at current premiums, still lead to deterioration in CWC.

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