A REVIEW OF AUSTRALIAN AND NEW ZEALAND SELECTION EXPERIMENTS FOR GROWTH AND FERTILITY IN BEEF CATTLE

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SUMMARY

The results of Australian and New Zealand selection experiments for growth and fertility in beef cattle are summarised and compared with evidence from other studies. Lines selected for a range of growth criteria generally showed consistent responses in weight and size at all ages, with no significant effects on fertility, maternal performance, dystocia rate or carcass maturity patterns. Limited evidence indicated positive correlated responses in feed conversion efficiency of breeding cows and growing steers. Divergent selection for calving rate resulted in responses in reproductive performance, but significant interactions with lactational status. Responses in lines selected for pubertal traits indicated favourable realised genetic correlations between scrotal size in bulls and age of first oestrus in heifers.

INTRODUCTION

Beef producers and researchers around the globe have been preoccupied with the prediction of the consequences of selection for many years. Much of the assumed knowledge of the consequences of selection comes from theoretical predictions based on estimates of genetic parameters obtained from the analysis of covariance between relatives. Only a small number of designed experiments have been conducted to provide empirical evidence of the responses to selection in beef cattle. During the past three decades several experiments have been conducted in Australia and New Zealand to investigate the direct and correlated responses to selection for growth and fertility traits in beef cattle. The results of most of these experiments were not included in previous reviews (e.g. Koch et al., 1982; Mrode, 1988) as they were only recently published or are still in progress. This review includes a brief summary of the design and major findings of these experiments, and compares the results with evidence from studies conducted in other countries.

SELECTION FOR GROWTH

(i) Selection for yearling weight and 18-month weight in Angus and Hereford cattle (Waikite)

An experiment was initiated at Waikite, near Rotorua, New Zealand, in 1971 to evaluate the responses to selection for increased yearling weight or increased 18 month weight in Angus and Hereford cattle (Baker et al., 1991). A Hereford line (HS1), and an Angus line (AS1) were selected for yearling (13-month) weight with first calving at 2 years of age; a second Angus line (AS2) was selected for 18-month weight with first calving at 3 years of age; and, a third Angus line (ACO) was maintained as a randomly bred control line. Table 1 includes various population parameters, selection differentials and direct responses for the lines up to 1986. After allowance for a small positive genetic trend in the ACO line the selection responses and realised heritabilities listed in Table 1 for the HS1, AS1 and AS2 lines increased by 30 to 40%. Slightly larger positive correlated responses were obtained for growth and carcass traits in the AS1 line than in the AS2 line (Morris et al., 1989; 1992). Positive responses were obtained in all lines for carcass fat depth at a fixed age, for feed intake and scrotal size of bulls, and for mature cow weight. Selection line differences from the ACO herd were not significant for female reproductive traits. The differences in carcass weight of bulls from the AS1 and ACO lines slaughtered at various ages were similar to differences in liveweight, with no line differences in dressing %, maturity patterns of carcass components, or in meat composition and tenderness (Morris et al., 1993a; 1994). Estimates of the pasture intake using "Captec Chrome" intra-ruminal controlled release devices (Nufarm Ltd, Australia) indicated that the AS1 cows tended to be more efficient than ACO cows in utilising feed for maintenance and calf growth (C. Morris, unpublished data).

Table 1. Population parameters, selection differentials and responses in lines of beef cattle selected for growth traits at Waikite, Trangie and Waikeria. †

	Waikite (1972-86)				Trangie (1974-92)			Waikeria (1964-81)	
Line [1]	ACO	AS1	AS2	HS1	Control	High	Low	PWG	YW
Generations of selection	3.35	4.85	3.78	4.60	4.99	5.48	5.07	6.3	5.6
Generation interval (years)	4.35	3.15	4.42	3.32	3.31	3.20	3.28	2.88	3.23
Number of bulls mated per year	10-12	6	5	6	10-12	5-6	5-6	5	5
Number of cows mated per year	125	165	125	165	50-100	85-120	85-120	125	125
Effective population size per generation	161.11	72.95	85.00	76.88	105.9	67.2	70.8	55.38	55.38
Average inbreeding rate (%) per generation	0.30	0.72	0.75	0.76	0.53	0.74	0.88	0.87	0.87
Average selection differential									
(for selected traits) kg per year		7.55	7.10	5.95		5.79	-6.72	5.00	6.45
phenotypic s.d.'s per year		0.33	0.23	0.26		0.207	-0.24	0.27	0.28
phenotypic s.d.'s per generation		1.04	1.02	0.86		0.641	-0.804	0.79	0.90
% per year		3.40	2.15	2.68		2.71	-3.15	5.70	2.46
Average selection response [2]									
(for selected traits) kg per year		2.49	1.70	2.16		2.11	-2.54	0.97	1.96
phenotypic s.d.'s per year		0.109	0.055	0.094		0.075	-0.091	0.053	0.084
phenotypic s.d.'s per generation		0.343	0.243	0.312		0.253	-0.304	0.153	0.271
% per year		1.12	0.52	0.97		0.87	-1.05	1.11	0.75
Realised heritability (for selected traits) [3]		0.31 ± .04	0.23 ± .05	0.33 ± .06		.37 ± .09	.38 ± .09	0.22 ± .06	0.34 ± .08

[1] Line codes - Waikite: ACO - Randomly selected control, Angus (still exists in 1994)
AS1 - High yearling weight, first calving at 2 y.o., Angus (still exists in 1994)
AS2 - High 18-month weight, first calving at 3 y.o., Angus
HS1 - High yearling weight, first calving at 2 y.o., Hereford

Trangie: Control - Randomly selected control, Angus
High - High growth from birth to 12 months of age, Angus
Low - Low growth from birth to 12 months of age, Angus

Waikeria: PWG - high post-weaning gain, Angus
YW - high yearling weight, Angus

[2] responses in the Waikite and Trangie selection lines were measured as deviations from the respective control lines; responses in the Waikeria lines were estimated from BLUP Animal Model analyses, with assumed heritabilities of 0.20 and 0.35 for PWG and YW, respectively.

[3] heritability estimates for the Waikite and Trangie lines were obtained from linear regression of direct response on cumulative selection differential, with the regression constrained to pass through the origin; estimates for Waikeria lines were obtained from paternal half-sib REML analyses

† References - Waikite: Baker et al. (1991); Trangie: Parnell et al. (1991), Parnell (unpublished); Waikeria: Carter et al. (1990)

(ii) Divergent selection for yearling growth rate (Trangie)

An experiment commenced at Trangie, NSW, in 1974 to investigate selection for growth rate in Angus cattle (Parnell et al., 1986). Divergent selection lines were established for either high (H) or low (L) growth rate to yearling age, along with a randomly selected control (C) line. Table 1 includes various population parameters, selection differentials and direct responses for the lines measured up to 1992. The divergence between the H and L lines in yearling growth rate was associated with correlated responses in weight and body size at all ages (Parnell et al., 1991). The H line heifers attained puberty earlier and had higher calving rates than C line heifers, whilst L line heifers attained puberty later and had reduced calving rates. The incidence of dystocia was lower for both H line and L line heifers (10% average) than for C line heifers (15% average). There was no difference between the H and C lines in mature cow calving rates, but a decline in the calving rate of L line cows. Cross-mothering and milk production studies indicated that about 18% of the divergence in calf weaning weights between the H and L lines could be attributed to maternal responses (Herd, 1990). Feed intake measurements indicated that the H line cows were more efficient than the C line cows in utilising feed for maintenance and calf growth, and the L cows tended to be less efficient (Herd, 1992). In addition, H line steers consumed less feed per kg liveweight to reach any particular weight than C line steers, and L line steers consumed more feed per kg liveweight. There were no line differences in the body composition of steers over a range of slaughter ages from birth to maturity (D. Perry, unpublished data).

Cows and calves from the H, C and L lines were also evaluated at Glen Innes, NSW, and Hamilton, Victoria, across a range of nutritional treatments. At Glen Innes, the pasture intake of cows and growing steers from each line and nutritional treatment were estimated at various times of the year using "Captec Chrome" intra-ruminal controlled release devices. Preliminary analyses (R. Dicker, unpublished data) indicated that, averaged across each treatment and sampling period, there were no differences between the lines in the ratio of calf weaning weight to cow's estimated dry matter intake. However, the ratio of weight gain to estimated pasture intake was higher for H line steers than for C and L line steers. At Hamilton, the H line cows weaned more calf weight per hectare than the C line cows at low stocking rates, and the L line cows weaned less calf weight per hectare. However, as stocking rate increased the difference between the lines in this measure of productivity tended to diminish (Graham et al., 1992). There were no significant genotype x environment interactions in the pre-weaning growth of H, C and L line calves measured at Trangie and at each of the nutritional environments imposed at Glen Innes and Hamilton (P. Parnell, unpublished data).

(iii) Selection for yearling weight and post-weaning gain (Waikeria)

Carter et al. (1990) described the results of a long-term selection experiment conducted at Waikeria, near Te Awamutu, New Zealand between 1964 and 1981. Selection lines for high post-weaning gain (PWG) from 5 to 13 months of age and for yearling weight (YW) at 13 months of age were established from an Angus herd of diverse genetic origin. Table 1 includes various population parameters, selection differentials and estimated responses for the lines. In the absence of a control line, genetic responses were estimated by Best Linear Unbiased Prediction (BLUP) analyses using assumed heritabilities estimated from this and other New Zealand data sets. BLUP genetic trends indicated that birth and weaning weights increased in the YW herd but not in the PWG line. Line crossing studies indicated no differences between the YW and PWG lines in cow maternal effects for birth weight or weaning weight, but increases in maternal effects after weaning in the PWG line.

(iv) Selection for growth rate in a tropical environment (Belmont)

A series of selection experiments were conducted at Belmont, near Rockhampton, Queensland, using a range of genotypes including a 100% Brahman line (B); a *Bos taurus* cross line (HS) containing 50% Hereford and 50% Shorthorn genes; a Brahman cross line (BX) containing 50% Brahman, 25% Shorthorn and 25% Hereford genes; an Africander cross line (AX) containing 50% Africander, 25%

Shorthorn and 25% Hereford genes; and a multi-breed line (AXBX), nominally consisting of equal contributions from Africander, Brahman, Hereford and Shorthorn (Burrow et al., 1991).

Seifert (1975a,b) described the results of an experiment conducted between 1963 and 1966 to evaluate the responses to a single generation of divergent selection for high or low growth rate to 18 months of age in the AX and BX populations. The progeny of the high growth rate lines in both populations were heavier at birth and had higher pre-weaning gains than progeny of the low growth rate lines. The cows selected for high growth rate also gained significantly more weight during their calves' pre-weaning period than the cows selected for low growth rate. Post-weaning responses in female progeny showed that the high line AX and BX animals also gained significantly more weight up to 18 months of age, with realised heritability estimates of 0.52 and 0.64, respectively.

Frisch (1981) reported the results of an experiment conducted between 1966 and 1977 to evaluate the consequences of selection for high postweaning growth rate. Responses in a closed HS line were measured as differences from an unselected control line. Liveweight increased at all ages in the selected line, except at birth where it declined relative to the control line. Animals sampled from the selected line had superior growth rates when exposed to environmental stresses due to heat, poor nutrition and infection with bovine keratoconjunctivitis and gastrointestinal helminths. However, they did not express superior growth rates at low levels of these stresses. Frisch (1981) concluded that the responses measured in the selected line were entirely due to increases in resistance to environmental stresses, and that the inherent growth potential of animals in the selected line had actually decreased.

A single generation selection experiment was conducted between 1983 and 1986 in which lines from each of the B, HS, AX, BX and AXBX genotypes were divergently selected for either high or low pre-weaning growth rate (Burrow et al., 1991a). Responses in liveweights at all ages were obtained in all genotypes, with the exception of birth weight in the HS genotype. Responses in pre-weaning growth rate were obtained in all genotypes, but post-weaning growth rates did not differ between the high and low lines in the B and BX genotypes. The realised heritability for pre-weaning gain, averaged over all genotypes was 0.17. Adaptive traits (i.e. parasite and heat resistance) did not differ between the lines, with the exception that parasite burdens increased in the high line of the more resistant AXBX genotype and were reduced in the high line of the more susceptible AX genotype. Cows allocated to the high line in each genotype reared more calves to weaning, had fewer neonatal mortalities and calved earlier than cows allocated to the low lines.

In 1985 a selection line was established in the AXBX population, with animals selected on the basis of BLUP Estimated Breeding Values (EBVs) for increased 600 day weight (Hetzel et al., 1988). A control line was also established with no net selection differential for 600 day weight EBV. After 6 years of selection there was a 6% increase in growth rate at pasture to 600 days of age in the selected line, with similar percentage increases in birth weight, weaning weight and scrotal size (G. Davis, unpublished data). Burrow et al. (1991b) reported that steers and heifers sampled from the selected line had higher weight gains than control line animals in the presence of environmental stresses at pasture, but there was no difference between the lines in weight gain or gross feed conversion efficiency when the animals were subsequently finished in a feedlot. When slaughtered at a similar carcass weight, animals from the selected line were leaner, but had similar levels of marbling and meat tenderness as the control line animals.

(v) Selection for pre-weaning growth rate in straight-bred and multi-breed populations (Wokalup)

An experiment was initiated in 1977 at Wokalup, near Bunbury, Western Australia, to examine the responses to selection for increased pre-weaning growth rate in a straight-bred Polled Hereford line and in a four-way cross multi-breed line (Wokalups) produced by mating Charolais x Brahman bulls with

Friesian x Angus or Friesian x Hereford cows. Embryos were collected from the foundation herds and stored for the future establishment of a control line (M. Carrick, pers. comm.). From 1978 to 1989 the lines were run separately as 12 single-sire breeding groups of about 25 cows each, with cows re-randomised into new paddocks each year (Lymbery et al., 1991). Replacement heifers and bulls were selected on individual pre-weaning growth rate up to 1985, and on BLUP EBVs for pre-weaning growth rate from 1986. After 12 years of selection the pre-weaning growth rate of calves had increased by approximately 0.12 kg per day (about 1% per annum) in both lines. BLUP estimates of genetic trend indicated that about 40% of the increase in growth rate in each line was due to genetic gain, with the remainder attributed to changes in environment, herd structure and management. However, these BLUP analyses assumed similar genetic parameters for the Hereford and the Wokalup lines. Subsequent analyses by Meyer et al. (1993) showed that the Wokalups had consistently more direct genetic variation, less maternal genetic variation, and less maternal environmental variation than the Herefords for all weights recorded between birth and 400 days of age. Attempts to re-establish the control line commenced in 1990, but problems in the storage and thawing of frozen embryos resulted in the survival of only a small number of animals (M. Carrick, pers. comm.).

(vi) Selection for growth in a large commercial open nucleus breeding scheme (Waihora)

Nicoll and Johnson (1986a,b) reported the results of a selection program in a large commercial Angus open-nucleus breeding scheme at Waihora, New Zealand. From 1976 to 1985 the scheme consisted of an average base population size of 26,000 cows, and a nucleus herd of 1100 cows. Selection of replacement bulls and heifers was primarily for a yearling index (YI) which incorporated calf weaning (WW) and yearling weights (YW), cow fertility (F) expressed as calves weaned per mating, and cow maternal weight at weaning (MW). The average generation interval in the nucleus herd was 3.76 years, and the average selection differentials on the index and its component traits were 0.28, 0.22, 0.27, 0.17 and 0.25 phenotypic standard deviations per year for YI, WW, YW, F and MW, respectively. BLUP estimates of genetic trend in the nucleus were 1.6 ± 0.9 and 0.7 ± 0.9 kg/year for WW and YW, respectively.

SELECTION FOR FERTILITY

(i) Selection for calving rate in a tropical environment (Lansdown)

An experiment was initiated at Lansdown, near Townsville, Queensland, in 1983 to investigate the responses to selection for cow fertility in the tropics (Hetzel et al., 1989). From a group of 600 Droughtmaster cows (approx. 50% Brahman, 50% Shorthorn), ranked on their BLUP EBVs for pregnancy rate, the 120 highest and 120 lowest ranking animals were allocated to high fertility (H) and low fertility (L) lines, respectively. These cows were joined to bulls also selected on pregnancy rate EBVs. During the first 3 years of the experiment there was a 12% average difference in pregnancy rate between the H and L line foundation cows. In lactating cows this difference was 17%, suggesting that lactational anoestrus was an important component of the line difference in fertility. The H line cows were lighter at mating and weaning than the L line cows and their body weight was less sensitive to seasonal fluctuations in nutrition. There was no difference in the birth weight, 12 month weight or 18 month weight of progeny from the foundation H and L line cows, but the H line calves were lighter at weaning. Hetzel et al. (1989) suggested that poorer milk production in the H line cows might explain the shorter periods of lactational anoestrus, earlier conception dates, higher pregnancy rates and lower calf weaning weights. Mackinnon et al. (1990) reported that male progeny of H line cows had larger scrotal sizes, and that heifer progeny had higher pregnancy rates, compared to progeny of L line cows. The H line progeny carried more gastro-intestinal worm eggs than L line progeny, but tick resistance and heat tolerance did not differ between the lines. Davis et al. (1993) reported that first generation H line heifers and cows had higher pregnancy rates and a shorter interval between mating and calving (days to calving) compared to L line females, with significant interactions between line, calving year and lactational status for both pregnancy rate and days to calving.

(ii) **Selection for pubertal traits in Angus cattle (Waikeria)**

Morris et al. (1993b) described an experiment initiated at Waikeria, New Zealand, in 1982 to investigate the responses to selection for pubertal traits in cattle, and to assess correlated responses in adult reproduction. Three selection lines and a control (C) line were established in an Angus herd that had previously been selected for growth traits. The first line (SC+) was selected for increased scrotal circumference in bulls at 13 months of age, with random selection of heifers; the second line (AGE-) was selected for reduced age at first oestrus in heifers and increased yearling (13 month) weight in bulls; and, the third line (AGE+) was selected for increased age at first oestrus in heifers and increased yearling weight in bulls. After 9 years of selection (approximately 2 generations) the average scrotal size of yearling bulls was increased by about 5.3% in the SC+ line, and the age of heifers at first oestrus was reduced by about 5.5%, compared to the C line. The age of heifers at first oestrus also differed between the AGE+ and AGE- lines (approx. 4.3%), but there was no difference in scrotal size between these lines. Correlated responses in heifer weight at first oestrus were in the same direction as changes in age at first oestrus in each line. At this early stage of the experiment there were no differences in adult reproduction evident between the lines. Since 1992, multi-trait BLUP procedures have been used to enable selection of both replacement bulls and heifers in the AGE+ and AGE- lines on the basis of EBVs for scrotal size and age at first oestrus.

DISCUSSION

There were more generations of selection, shorter generation intervals, higher selection differentials and larger effective population sizes in the long-term growth selection experiments conducted at Waikite, Waikeria and Trangie compared with most of the beef cattle selection studies reviewed by Mrode (1988). The direct selection responses were similar to the average of 0.8% per year reported by Mrode (1988), but less than the estimate of 1.44% predicted by Smith (1984) for yearling weight in a large theoretical population. This discrepancy can largely be attributed to the shorter generation interval assumed by Smith (1984). Considering the potential for errors in the prediction of selection responses from base population genetic parameters, and in the measurement of realised responses from unreplicated selection experiments, there was good agreement between the predicted and the empirical responses obtained in these experiments. The realised heritabilities obtained for yearling weight and yearling growth rate were similar for the selection lines at Waikite and Trangie, particularly after correction for apparent genetic trend in the Waikite control line. These values also corresponded closely with heritability estimates obtained from paternal half-sib analyses of the Waikeria yearling weight selection line (Carter et al., 1990) and REML animal model estimates from the Trangie data (Meyer, 1992; and, Parnell, unpublished data), but were lower than REML animal model estimates obtained from the Waikite data (Baker et al., 1986). The realised heritabilities were also consistent with those obtained in other beef cattle yearling weight selection lines (Mrode, 1988), and with the average of 0.39 reported by Woldehawariate et al. (1977) from a summary of literature values.

Due to the lack of replication, the interpretation of correlated responses from beef cattle selection experiments is often considered ambiguous. However, the correlated responses measured in these experiments were remarkably consistent. Each of the growth selection experiments showed positive responses in liveweight at all ages, with the exception of birth weight in lines of Hereford x Shorthorn cattle selected for either postweaning growth rate or weaning weight in a tropical environment at Belmont. Apart from this exception, the responses were in general agreement with the results of other beef cattle growth selection experiments (Mrode, 1988) and confirm previous estimates of positive genetic correlations between liveweight at different ages (Woldehawariate et al., 1977). The variation in patterns of direct and correlated selection responses in adapted and non-adapted breed types at Belmont indicate possible G x E interactions in this environment. The maternal components of the correlated responses in pre-weaning growth measured at Trangie were higher than estimates from the Waikite and Waikeria selection lines; smaller than that estimated by MacNeil et al. (1992) for an inbred Hereford line selected mainly for postweaning growth; but similar to that estimated by R.M. Koch (pers. comm.) for Hereford lines selected for yearling or weaning weight. These differences may partly be due to differences in the absolute importance of maternal ability on the expression of growth among the various breeds and environments, and partly due to differences in the magnitude and sign of genetic correlations between the direct and maternal effects. Meyer (1992) and Waldron et al. (1993) found low positive genetic correlations between direct and maternal effects in the Trangie and Waikite selection lines, respectively. This contrasts with reports of zero or slightly negative genetic correlations between direct and maternal effects in other populations (Meyer, 1992). The increased genetic variation and potential for selection response evident in the Wokalup multi-breed line, compared to the straight-bred Polled Hereford line, is consistent with the results of a similar comparison of the rates of genetic gain in straight-bred and multi-breed synthetic populations in Alberta (Sharma et al., 1985).

The lack of significant correlated responses in carcass traits at any slaughter age corresponds with most of the limited evidence available from other selection experiments (Mrode, 1988), but differs from the suggestion by Koch et al. (1982) that selection for increased growth rate in a feedlot would result in a small increase in fatness at a constant age. It is possible that the level of feeding during the finishing phase may affect the correlated responses in carcass fatness (Baker and Morris, 1984). Indicators of reproductive performance, calving ease and survival in each of the growth selection lines were either improved or not significantly different from the respective control populations. This is consistent with the evidence from most other selection studies, with the major exception being an experiment conducted in Nebraska where heifer dystocia and calf mortality rates increased significantly in Hereford lines selected for increased weaning or yearling weight (Koch et al., 1982). However, the environment and management system in the Nebraska experiment were very different to those in the Australian and New Zealand studies, and the base level of dystocia was substantially higher. In the Trangie high growth rate line the pelvic area of first-calf heifers tended to increase at a greater rate than the birth weight of their calves (Parnell, unpublished data), possibly contributing to the observed reduction in dystocia rate. The responses in pubertal age of heifers in the Trangie selection lines were consistent with the expectation from published genetic correlation estimates (Morris, 1980), though no differences in the age at puberty were apparent in the Waikitie growth selection lines.

The improvements in postweaning gross feed conversion efficiency measured in the Trangie and Belmont growth selection lines corresponded with the findings of North American studies (Koch et al., 1982). These responses were also consistent with the observed growth responses in lines selected for improved gross feed conversion efficiency (e.g. Mrode et al., 1990; Bishop et al., 1991). Direct measurements of the feed intake at Trangie and estimates of pasture intake at Waikite also indicated improvements in feed conversion efficiency of breeding cows in the high growth selected lines. Estimates of the pasture intake of the Trangie lines across a range of nutritional treatments at Glen Innes did not reveal any line differences in cow efficiency, but there was a low repeatability (0.3) between the estimated pasture intakes of individual cows at different sampling periods (R. Dicker, pers. comm.). In each of the above studies, there was a large variation in feed intake and efficiency between cows within each line, independent of differences in cow weight.

The selection experiments for pregnancy rate at Lansdown and for pubertal traits at Waikeria are among the few studies ever conducted on selection for reproductive performance in beef cattle. The use of within-breed selection to improve fertility has generally been disregarded because of the low heritability estimates obtained for most reproductive traits. The Lansdown experiment demonstrated that permanent differences in fertility could be obtained from a single round of divergent selection in *Bos indicus* cattle in a tropical environment, and that interactions with lactational status influenced the realised responses. Pubertal measurements on first-generation progeny indicated that selection for pregnancy rate may have accelerated sexual maturity in both heifers and bulls (Mackinnon et al., 1990).

Unfortunately, due to the lack of a control line in this experiment it was not possible to quantify how much of the observed responses were due to increased fertility in the high line and how much was due to successful selection for poor fertility in the low line. Early results of the Waikeria experiment tend to confirm the existence of favourable genetic correlations between male and female pubertal traits, but it is too early to detect any measurable responses in adult reproductive performance.

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