Undesirable side effects of selection for high production efficiency in farm animals: a review

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Abstract

Genetic selection has increased production levels of livestock species considerably. However, apart from a favourable increase in production, animals in a population that have been selected for high production efficiency seem to be more at risk for behavioural, physiological and immunological problems. Examples are presented of over 100 references on undesirable (cor)related effects of selection for high production efficiency, with respect to metabolic, reproduction and health traits, in broilers, pigs and dairy cattle. A biological explanation for the occurrence of negative side effects of selection is presented. Genetic selection may lead to loss of the homeostatic balance of animals, resulting in the occurrence of pathologies and consequently in impaired animal welfare. Future application of modern reproduction and DNA-techniques in animal breeding may increase production levels even faster than at present, which may result in more dramatic consequences for behavioural, physiological and immunological traits. Selection for more than production traits alone may prevent such. Without knowledge about the underlying physiological processes on which genetic selection acts, selection is essentially a black box technique. Knowledge of biological backgrounds will offer the opportunity to understand, anticipate and prevent undesirable side effects of selection. © 1998 Elsevier Science B.V.

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1. Introduction

Genetic selection has increased production levels of livestock species considerably. Since feed costs are economically the most important costs, the breeding goal in most livestock species is to create a population with high economic production efficiency, i.e. high production combined with relatively low feed intake (Luiting, 1990).

Breeding programs have become quite successful because of the high accuracy of breeding value estimation, the moderate to high heritabilities of most production traits and the use of large and fast databases containing production records of many animals and their genetic relationships. Apart from

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genetic changes, production is also increased by improvement of environmental factors such as housing, feed composition, feeding strategies, health status and farm management. Rapidly developing techniques in farm animal reproduction and new molecular technologies will increase in the near future the intensity and accuracy of selection even more.

However, apart from desired effects of genetic selection focused on high economic production efficiency, negative side effects have become apparent. Animals in a population that have been genetically selected for high production efficiency seem to be more at risk for behavioural, physiological and immunological problems.

This paper presents examples of undesirable (cor)-related effects of selection for high production efficiency in broilers, pigs and dairy cows. A possible biological explanation and implications for genetic selection are discussed.

2. Genetic change and correlated responses to selection

Selection for high production efficiency may result in correlated responses in other traits. The current theory about correlated selection responses is well documented in textbooks (e.g. Pirchner, 1983; Falconer and Mackay, 1996). Briefly, the observed phenotypic association (r_p) between trait 1 and 2 is a function of the underlying genetic correlation (r_g) and the environmental correlation (r_e), which can be written as: $r_p = h_1 h_2 r_g + e_1 e_2 r_e$, where $e_x = \sqrt{(1 - h_x^2)}$ and h_x^2 is the heritability of trait x. The genetic correlation expresses the extent to which two characters are genetically associated; the environment is a cause of association when two characters are influenced by the same differences of environmental conditions. It follows that the phenotypic correlation depends, besides genetic and non-genetic correlations between traits, on the heritability of each trait, i.e. the proportion of the total variance which is caused by genetic variation among animals. Genetic and environmental correlations can differ in magnitude and sign and thus the phenotypic correlation that can be observed gives no conclusion about the magnitude and sign of the genetic correlation. The

correlated response in trait 2 when selection is for trait 1 can be predicted by $CR_2 = i h_1 h_2 r_g \sigma_{p2}$, where i is the intensity of selection and σ_{p2} represents the phenotypic standard deviation of the correlated trait. The formula shows that the genetic correlation (r_g) accounts for the sign and partly for the magnitude of the correlated selection response and is consequently the interesting parameter when assessing genetic side effects of selection.

The current animal breeding theory distinguishes two causes of genetic correlation between traits: linkage and pleiotropy. Linkage is the situation in which different loci influencing separate traits are situated close together on the same chromosome, preventing the genes from segregating independently at meiosis. Pleiotropy is the situation where a single gene affects two or more different traits. Production traits are usually composed of many underlying synchronously proceeding co-operative metabolic processes, each of which is more or less genetically determined. The biochemical reactions and control mechanisms on which a gene and thus genetic selection acts, are likely to influence more than one trait. The actual genetic correlation between two traits is the net effect of pleiotropy and linkage. Falconer and Mackay (1996) state that estimates of genetic correlations are usually subject to rather large sampling errors and are therefore seldom very precise; moreover they may differ in different populations since the genetic correlations are strongly influenced by allele frequencies.

Genetic side-effects of selection may be assessed from selection experiments or from estimated genetic relationships between the traits of interest. Data obtained from selection experiments are mostly on experimental animals kept under relatively similar and constant conditions which consequently reduces the environmental variation. Most selection experiments include a control line and/or two divergently selected lines in order to separate correlated genetic responses from environmental changes. However, due to long generation intervals and high experimental costs in larger livestock species, observations may be on few animals only, selected for relatively few generations. In those species, most information is based on field data and thus subject to management policy, herd size, season, age, breed, etc. (Grommers, 1987). Advanced statistical techniques attempt to

account for these environmental effects, but they estimate genetic parameters under the assumption of a simplified linear model which can produce no more than an approximation of the true state of nature.

In practice, realised heritabilities for traits under selection in commercial broilers, pigs and dairy cows seem to remain positive, resulting in a continuous positive selection response for production traits. This gives, however, no conclusion about the future state of the animal as will become clear from the reviewed side-effects of selection: e.g. selection for high body weight in turkeys has led to a continuous increase in body weight, but also resulted in extremely heavy male animals that make natural mating impossible.

Several long term selection experiments, especially in mice, did show limits to selection (Eisen, 1980; Barria and Bradford, 1981; Bünger et al., 1984; Canon et al., 1992), supporting the statement of Falconer and Mackay (1996) that response of selection can not be expected to continue indefinitely. Several reasons have been postulated why limits to selection for traits under selection have not yet been reached in commercial livestock species as compared to experimental results. Commercial selection has been less intense than that applied in selection experiments. Moreover, an aggregate genotype consisting of several traits will prolong the expected period of response (Fredeen, 1984; Hunton, 1984). Improved management and quality of the environment reduces environmental variability allowing for relatively greater expression of genetic variability, and thus increased estimated heritabilities.

Application of modern techniques will alter the speed at which genetic increase in production is achieved. Rapidly developing techniques and commercial use of *in vitro* maturation and fertilisation, gene transfer, sperm and embryo sexing and embryo cloning will increase the intensity of selection. New molecular technologies, allowing the livestock breeders to select on genotype rather than on phenotype, will increase the efficiency of selection in farm animals and the rate at which genetic gains will be achieved even more (Hansel and Godke, 1992). Gene mapping and marker assisted selection will enable selection early in life unaffected by micro-environmental variation, equally in both sexes, and without requiring costly trait evaluation, which will increase intensity and accuracy of selection and

decrease generation interval (Soller, 1994). However, it will also increase the speed of expression of detrimental antagonistic relationships with selection for high production efficiency.

In order to anticipate undesirable genetic correlated responses to selection, those have to be described first. In this review, examples in the literature on undesirable genetic side effects of selection and on genetic correlations between production traits and metabolic, reproduction and health traits will be discussed. Three livestock species are considered with one product each: meat type poultry, meat type pigs and dairy cattle.

3. Undesirable side-effects to selection for high production efficiency

3.1. Broilers and turkeys

3.1.1. Responses in production traits

The primary aim in poultry meat production is rapid growth, superior feed efficiency and high processing yield. Poultry breeding animals have shown a continuous response to selection for growth rate with heritabilities of approximately 40% (Cahaner and Siegel, 1986). Moreover, application of quantitative genetic and biometrical methods to poultry breeding has resulted in a genetic increase in production efficiency (Reddy, 1996). About 85 to 90% of the increase in body weight resulted from genetic selection for increased body weight (Havenstein et al., 1994a).

Table 1 shows the increase in production in broilers and turkeys from 1960 to 1996. Age at a given body weight in broiler chickens is reduced (Cahaner and Siegel, 1986) by about 1 day per year (Havenstein et al., 1994a).

3.1.2. Responses in metabolic traits

The genetic increase in production has been supported by a corresponding correlated genetic increase in daily feed consumption (Dunnington and Siegel, 1995) and feed efficiency (Owens et al., 1971; Marks, 1979; Barbato et al., 1984; Havenstein et al., 1994a; Dunnington and Siegel, 1995). It appears that in general most of the heritable variation in body weight gain is associated with differences in

Table 1
Means of age at slaughter (AGE), liveweight at slaughter (SW), feed conversion (FC) and growth rate (GR) in broiler chickens (B) and turkeys (T) from 1960 to 1996

Trait	1960	1965	1970	1975	1980	1985	1990	1995	1996
AGE[b] (B) (d) (NL)		59	51	48	49	46	45	43	44
SW[b] (B) (g) (NL)		1250	1330	1420	1560	1630	1790	1860	1900
SW[c] (B) (g) (USA)	1680	1745	1820	1880	1975	2095	2185	2330	
SW[d] (T) (kg) (USA)	7.53	8.21	8.92	8.88	9.26	10.03	10.63	11.58	
FC (B)	2.5[a]	2.32[b]	2.10[b]	2.03[b]	2.04[b]	2.0[a,b]	1.92[b]	1.83[b]	1.83[b]
GR (B) (g/d)	10[a]	21[b]	26[b]	30[b]	33[b]	37[b], 40[a]	42[b]	44[b]	45[b]

[a], Cahaner and Siegel (1986); [b], LEI-DLO (1996); [c], USDA (1995a); [d], USDA (1995b).

feed intake (McCarthy and Siegel, 1983). Dunnington and Siegel (1996) reported that superior feed efficiency of a high body weight line over a low body weight line, in a divergent selection experiment for body weight in broiler chickens at 8 weeks of age, was associated with several physiological factors, including a decrease in metabolic rate as measured by oxygen consumption (Owens et al., 1971), a higher rate of food passage and digestion (Cherry and Siegel, 1978; Dunnington and Siegel, 1995) and higher enzymatic activities in the small intestine (Dunnington and Siegel, 1995). Lepore et al. (1963) observed a more efficient utilisation of energy and the amino acid histidine in embryos of the high body weight line compared to the low body weight line.

Both the high and the low body weight line differed for several traits related to appetite (Dunnington and Siegel, 1996). Experimental lesions made in the hypothalamus of hens from both lines resulted in an expected obesity syndrome in the low body weight line, but not in the high body weight line. This suggests that selection for increased body weight damaged the hypothalamic satiety mechanisms leading to a failure to diminish the hunger drive and consequently to hyperphagia or overconsumption (Burkhart et al., 1983). These results are supported by an experiment using the force feeding technique, which forces chickens to eat more than their ad libitum feed intake: chickens from the low body weight line could be fed substantially above ad libitum feed intake, whereas in the high body weight line this was possible to a significantly lesser extent. At day 1 of age, chickens of the high body weight line could not be overfed, whereas the low body weight line could be fed 150% above ad libitum;

during the first 3 weeks of age the high body weight line and the low body weight line could be fed 10% and 23% above ad libitum feed intake, respectively. The results suggest that chickens selected for high body weight are inclined to eat a volume of feed corresponding to the size of their gastro-intestinal capacity: they consume feed above their metabolical requirements until they reach a limit set by their gastro-intestinal capacity (Barbato et al., 1984; Nir et al., 1978). Denbow et al. (1986) showed increased appetite in a high body weight line compared to a low body weight line as a result of increased responsiveness to biogenic amines, which regulate food intake.

Intense selection pressure for body weight in broilers has altered the growth pattern so that birds reach slaughter weights at younger ages (Marks, 1979; Anthony et al., 1991). High body weight line chickens grew faster and had a higher percentage of body fat than the low body weight line (Chambers et al., 1981; Barbato et al., 1984; Dunnington and Siegel, 1996) and compared to a randombred line (Havenstein et al., 1994b). The higher percentage of body fat in the high body weight line resulted mainly from decreased rates of lipolysis (Calabotta et al., 1985). It is suggested that excessive fat deposition in chickens selected for rapid growth is associated with increased concentrations of insulin and glucagon in plasma and perhaps insulin resistance (Sinsigalli et al., 1987).

3.1.3. Responses in reproduction traits

Selection for fast growth rate has resulted in correlated negative responses for several reproduction traits. A dramatic consequence of long-term selection for increased muscle in turkeys is the

damage made to the back of the hens by the heavy males with natural mating. One hundred percent artificial insemination allowed for the continuation of intense selection for body weight in male lines (Hunton, 1984; Cahaner and Siegel, 1986; Dunnington, 1990). Fertility is reduced in broiler breeder hens with excessive body weight (Dunnington, 1990; Liu et al., 1995). It is generally accepted that reproductive problems are common in broiler strains, and husbandry practices are routinely employed to reduce adult body weight (McCarthy and Siegel, 1983).

Broiler breeders selected for high body weight produced a higher number of eggs than broilers selected for low body weight, but a higher percentage of defective eggs (e.g. double yolk, extra-calcified, shell-less, soft shelled): 17.1 and 2.4% in the high and the low body weight line, respectively (Van Middelkoop and Siegel, 1976; Anthony et al., 1989). This increase in number of defective eggs produced was in large part due to lost synchrony of ovulation and packaging of the eggs (Dunnington and Siegel, 1996). The high body weight line showed an increased 'erratic ovulations and defective egg syndrome' (EODES) quantified by the ratio of percentage daily production of normal eggs (DP) over percentage daily ovulation (DO) (Jaap and Muir, 1968; Siegel and Dunnington, 1985; Liu et al., 1995). Ratios of DP:DO were for the high and the low body weight line 0.84 and 0.98, respectively (Anthony et al., 1989; Liu et al., 1995). Percentage hatch of fertile eggs decreased significantly with 1.11% per generation in broilers selected for 15 generations for high 12-week body weight (Maloney et al., 1967). Embryos of a high 8-week weight selected broiler line revealed a higher frequency of chromosomal abnormalities (14.5%) than a line selected for low body weight (6.2%) (Reddy and Siegel, 1977).

Inconsistent results have been reported on the effects of selection for high body weight on several semen characteristics. Marini and Goodman (1969) found a lower semen concentration, volume and motility and higher percentage dead and abnormal sperm cells in a high 12-week weight selected line compared to a low weight selected line of broilers in generation 15. In generation 18, however, only sperm concentration was reported to be significantly

different (Cheng and Goodman, 1976). Nestor (1977) observed a lower semen concentration and volume in 16-week body weight selected turkeys compared to a randombred control line. Siegel (1963) observed a *higher* semen volume in high 8-week weight selected broilers compared with low weight selected broilers; motility was lower and no differences in semen concentration were found. Edens et al. (1973) showed that spermatozoa of a high body weight line possess a lower potential for a sustained endogenous metabolism than the spermatozoa of a low body weight line, which may be related to the lower sperm motility found in the high body weight line.

3.1.4. Responses in health traits

Selection for high body weight has resulted in a correlated negative immune performance. Broilers selected for high growth rate showed lower antibody responses when challenged with sheep erythrocytes (SRBC) than a low body weight line (Miller et al., 1992) and a randombred control line (Qureshi and Havenstein, 1994). Little or no differences were found between lines in macrophage and natural killer cell functions, i.e. the non-adaptive components of the immune system (Qureshi and Havenstein, 1994). Nestor et al. (1996a), Nestor et al. (1996b) found a significantly higher percentage of mortality in turkeys selected for high 16-week body weight compared to a randombred control line in a natural outbreak of erysipelas, 11.8 and 1.6% respectively, and when challenged with either *Pasteurella multocida*, 72.1 and 43.6% respectively, and Newcastle disease virus, 32.5 and 15.8% respectively.

Havenstein et al. (1994a) reported a more than four times higher mortality at 42 days of age in a commercial 1991 broiler strain (9.7%) as compared to a randombred baseline originating from 1957 (2.2%). The lines used in this experiment did not originate from the same population. Most of the mortality in the commercial strain after 3 weeks of age was associated with flipovers (sudden death), ascites and leg problems. Moreover, incidence of tibial dyschondroplasia was 47.5% in the commercial line compared to 1.2% in the randombred baseline. The lines differed greatly in severity of the lesions: in the commercial line, 42.4% of the lesions involved more than one-fourth of the tibial head, whereas in

the randombred line all lesions involved less than one-fourth of the tibial head. Leenstra (1993) indicated that male chickens from a line selected for high body weight at 6 weeks of age showed more cases of severe dyschondroplasia (28%) than male chickens from a line selected for low feed conversion (3%). Moreover, broilers selected for high body weight had a higher mortality rate (7.4%) than broilers selected for low feed conversion (2.0%) which was mainly caused by infectious diseases and heart and circulation problems.

Ascites, i.e. the accumulation of edematous fluid within the abdominal cavity, is a disease found at high altitutes under hypoxic conditions. Since approximately 1980 ascites in broiler chickens is also observed at lower altitudes, even at sea level. In The Netherlands, ascites, as a cause of mortality in broiler chickens, is increasing steadily, running parallel with a faster growth rate and, as a result, an increasing metabolic rate (Scheele, 1996). A high incidence of heart failure syndrome and ascites was found in fast growing broilers exhibiting a low feed conversion ratio resulting from low values of heat production per gram body weight gain and oxygen consumption per gram deposited protein (Scheele, 1996). Heart failure syndrome and ascites may be initiated by a limited thyroid hormone production of which the main effect is to increase metabolic rate by stimulating oxidative metabolism (Scheele et al., 1992). Havenstein et al. (1994b); Dunnington and Siegel (1995) observed a decreased heart and lung size as a percentage of body weight with genetic selection for increased growth rate. It is suggested that faster growth in broiler chickens requires more oxygen to support the higher metabolic rate. If oxygen becomes a limiting factor, the same diseases may occur as are known under hypoxic conditions, like heart failure and ascites (Scheele, 1996).

The metabolic properties of a muscle are related to the ability of an animal to cope with environmental stresses: muscles with a high endurance capacity, low proportion of white glycolytic fibres, high capillary supply, high oxidative capacity and smaller fibres are better in conserving their energy than muscles with the opposite characteristics and consequently better able to sustain environmental stresses (Henckel, 1992). It appears that in pigs, the glycogen level in muscles may be more related to PSE (pale,

soft and exudative meat) proneness, which is preceded by PSS (Porcine Stress Syndrome), than halothane sensitivity (Henckel et al., 1992). Henckel (1992) observed a surprisingly low proportion of oxidative slow twitch muscle fibres and a high proportion glycolytic fast twitch fibres in different muscles of chickens. This suggests that most commercial chickens may be very sensitive to environmental stresses, resembling the situation observed in pigs. Indeed those muscles in the chicken would be classified as PSE (Henckel, 1992) as has been observed in turkeys (Barbut, 1997). Henckel (1992) suggests that since glycolytic fast twitch muscle fibres have higher growth potentials than other fibre types, the increase of glycolytic fast twitch fibres may be a result of selection for high growth rate.

Turkeys selected for high 16-week body weight required fewer inductions to reach a longer duration of tonic immobility than birds from a randombred control line implying a higher state of fearfulness in the high body weight line (Nestor et al., 1996a).

3.2. Pigs

3.2.1. Responses in production traits

In pig production, selection is mainly on high growth rate and/or minimum backfat thickness, i.e. high lean tissue growth rate, on low feed conversion, soundness and recently also litter size. A continuous increase in growth rate and decrease in feed conversion is shown in Table 2 from 1960 to 1996 in Dutch and Norwegian meat type pigs. Dutch figures originate from on farm testing, Norwegian figures originate from sib-testing on sisters and castrates on testing stations. Because in breeding programmes much emphasis is placed on production traits, and heritabilities are moderate (growth rate, feed conversion) to high (meat percentage), the increase in production efficiency is probably to a high extent of genetic origin.

3.2.2. Responses in reproduction traits

Under normal conditions a sow shows oestrus between 4 and 7 days after weaning, but the time from weaning to oestrus is highly variable, especially in first-litter sows, and may be 200 days or longer (Ten Napel, 1996). Analyses of data from pigs selected for high daily gain and low backfat within

Table 2
Means of growth and feed conversion (FC) in Dutch (NL) and Norwegian (N) meat type pigs from 1960 to 1996

Trait	1960	1970	1974	1977	1980	1983	1986	1989	1992	1995	1996
Growth (g/d) (NL)[a]			606	611	646	651	693	718	717	729	
Growth (g/d) (N)[b]	629	706			835	888	897	936	960	956	962
FC (NL)[a]			3.39	3.27	3.15	3.08	2.98	2.93	2.87	2.79	
FC (N)[b]	3.24	2.83			2.54	2.50	2.45	2.31	2.26		

[a], IKC (1996); [b], Norsvin (1996).

two farms showed no clear genetic relationship with incidence of prolonged intervals from weaning to farrowing when only sows with an observed interval were included. However, when sows that were culled after normally weaning a litter were supposed to be culled for anoestrus, and were included into the analyses as having a prolonged interval, genetic relationships between rebreeding performance and the traits under selection were consistently unfavourable and mostly significant. Large White pigs with a prolonged interval from weaning to farrowing had a 14.6 g/d higher breeding value for average daily gain and a 0.64 mm lower breeding value for backfat adjusted for body weight (Ten Napel and Johnson, 1997). Genotype does not affect the weaning-to-oestrus interval in a direct way, but acts in an indirect way through genetic variation in susceptibility to factors prolonging 'interval weaning to start of cycle'. It is stated that genetic variation in susceptibility to severe depletion of body reserves and stressors may explain the observed genetic variation in weaning-to-oestrus interval (Ten Napel et al., 1995).

Genetic correlations between daily growth rate, lean percentage and backfat, and several reproduction traits are presented in Table 3. Hutchens et al. (1981) defined puberty as first detected oestrus indicated by a standing response to a boar; in the two other studies, puberty was defined as the first ovulation judged by progesterone levels. Pro-oestrus was defined as the period before standing oestrus when reddening and swelling of the vulva was observed, and length of standing oestrus was defined as the number of days that the gilt showed a standing reflex. Gilts with higher lean percentage had genetically delayed onset of puberty, showed shorter pro-oestrus, less intense and shorter reddening and swelling of the vulva at puberty, and had a higher ability to show standing reflex. Kirkwood and Aherne (1985) suggest that selection for leanness is also selection for a larger mature size and, on a chronological time scale, a physiologically younger

Table 3
(a) Genetic correlations between daily growth rate, lean percentage and backfat, and several reproduction traits in pigs; (b) Number of animals (*N*), breed, average growth rate, lean percentage and backfat

a	Trait	Daily growth rate	Lean percentage	Backfat
	Intensity vulvar symptoms	0.19[c]	− 0.17[c]	
	Duration pro-oestrus (d)	0.03[c]	− 0.09[c]	
	Standing reflex	− 0.61[c]	0.10[c]	
	Duration standing oestrus (d)	− 0.49[c]	0.02[c]	
	Age at puberty (d)	− 0.38[a], − 0.31[b], − 0.07[c]	0.20[b], 0.40[c]	0.27[a]
	Age at farrowing	− 0.61[d]		− 0.16[d]
	Piglet weight	0.50[a], 0.41[b]	0.14[b]	0.19[a]

b	*N*	Breed	Average Growth rate (g/d)	Average Lean %	Average backfat (mm)
[a]	737	D, Y, S, LR gilts	690 (weaning–90.7 kg)		25.2 (90.7 kg)
[b]	393	Y gilts	823 (25–90 kg)	58.5 (90 kg)	
[c]	740	Y gilts	832 (25–90 kg)	58.2 (90 kg)	
[d]	4068	Y sows	525 (birth–80 kg)		11.9 (80 kg)

[a], Hutchens et al. (1981); [b], Rydhmer et al. (1992); [c], Rydhmer et al. (1994); [d], Rydhmer et al. (1995).
D, Duroc; Y, Yorkshire; S, Spot; LR, Landrace.

animal. Selection for increased growth rate, efficiency and leanness appears to have resulted in an increase of some 30% in mature size over 20 years (Whittemore, 1994). If a minimum percentage body fat is required for the onset of oestrus, puberty can be expected to be delayed. However, Hutchens et al. (1981) found a positive genetic correlation between body weight adjusted backfat (which is inversely related to leanness) and age at puberty.

Growth rate was genetically negatively correlated with the ability to show standing reflex, duration of standing oestrus and onset of puberty, and positively with the intensity of vulvar symptoms. When genetic correlations between growth rate and oestrus traits and leanness and oestrus traits have opposite signs, the consequence of selection for high lean tissue growth rate on oestrus traits will depend on the relation between growth rate and leanness in the breeding goal (Rydhmer et al., 1994, 1995).

Piglet weight, which is positively related to piglet survival, growth of slaughter pigs and litter size of breeding sows, was positively correlated with both growth rate and lean percentage (Rydhmer et al., 1992). However, Hutchens et al. (1981) observed a positive genetic correlation between backfat and piglet weight. Kerr and Cameron (1995) observed that selection for lean growth did not significantly affect reproductive performance, but that animals selected for high lean food conversion or low daily food intake had reduced reproductive performance: litter size and weight at birth were reduced in the high lean food conversion line (9.1 vs. 10.7 kg) and the low daily food intake line (9.6 vs. 10.2 kg) compared to their corresponding control lines (10.7 vs. 13.7 kg and 11.1 vs. 13.7 kg, respectively).

Between-study variation in sign and magnitude of the genetic correlations between production traits and reproduction traits may result from the fact that the parameter estimates are experiment specific and from differences in selection strategies, populations and environments within the studies (Kerr and Cameron, 1996). Moreover, trait definitions may vary between studies (Rydhmer et al., 1992).

3.2.3. Responses in health traits

Lacombe boars selected for high lean tissue growth rate in an experiment of Sather (1987) showed significantly more leg weakness in the foreleg (29.5%) and rear leg (41.5%) than non-

selected control boars (18.4 and 28.1%, respectively). Average daily growth rate from 56 days of age to 90 kg body weight was 861 and 777 g, and average backfat adjusted to 90 kg body weight 15.6 and 16.3 mm for selection line and control line boars, respectively. Effects in gilts were smaller and only significant for foreleg scores (9.2 and 3.6% for selected and control line gilts, respectively). Front-end structural leg soundness scores in barrows and gilts were not significantly affected by selection in the 5th generation of a divergent selection experiment for postweaning average daily body weight gain (Woltmann et al., 1995). The selection differential for divergence was 470 g/d or approximately five standard deviations.

Leg weakness can be to some extend explained by the occurrence of osteochondrosis. Table 4 shows genetic correlations between production traits and leg weakness and osteochondrosis (OC) scores. Pigs with high leanness and growth rate had worse leg scores, and worse OC scores in both the elbow and the knee joint (Lundeheim, 1987; Huang et al., 1995). Webb et al. (1983) found in a group of 23 975 Large White and Landrace boars adverse genetic correlations of −0.20 to −0.40 between fat depth measurements and aggregate leg scores which represented both the number and severity of several leg problems.

More oxidative intermediate and oxidative slow twitch muscle fibres have been found in the *Longissimus dorsi* muscle in wild pigs compared to domesticated pig breeds by Rahelic and Puac (1980) and Essén-Gustavsson and Lindholm (1984), respectively. Moreover, oxidative capacity was significantly higher and glycogen content significantly lower in wild boars. They had significantly larger mean fibre areas, a larger number of capillaries per fibre, and higher oxidative enzyme activities (Karlström, 1995). These results may indicate that domestication of pigs has resulted in a decreased ability to sustain environmental stresses. Investigation into direct effects of selection for high growth rate on muscle composition is desired.

3.3. Dairy cattle

3.3.1. Responses in production traits

In most dairy cattle breeding programs, selection is mainly for high milk yield. Table 5 shows the

Table 4

(a) Genetic correlations between lean percentage and growth rate, and leg weakness score and osteochondrosis score for elbow and knee; Number of animals (*N*), breed, average growth rate and lean percentage

a	Trait	Lean percentage	Daily growth rate	
	Leg weakness score (0–5)[d]	− 0.43[a], − 0.09[b]	− 0.26[a], − 0.35[b], − 0.39[c]	
	Osteochondrosis elbow score (0–5)[e]	0.22[a], 0.17[b]	0.10[a], 0.19[b]	
	Osteochondrosis knee score (0–5)[e]	0.28[a], 0.08[b]	0.29[a], 0.03[b]	
b	*N*	Breed	Average growth rate (g/d)	Average lean percentage
a	5568	LR	883 (30–100 kg)	59.1 (100 kg)
b	4318	Y	897 (30–100 kg)	59.1 (100 kg)
c	2257	LR, Y, D	888 (30–110 kg)	

[a], [b], Lundeheim (1987); [c], Huang et al. (1995).
[d], 0 = worst, 5 = best.
[e], 0 = best, 5 = worst.
Y, Yorkshire; LR, Landrace; D, Duroc.

Table 5

Means of milk production per lactation (MP) and days in milk per lactation (DIM) in The Netherlands (NL), Norway (N) and United States (USA) from 1950 to 1996

Trait	1950	1955	1960	1965	1970	1975	1980	1985	1987	1989	1991	1993	1996
MP (kg) (NL)[a]	4029	4118	4372	4370	4639	5063	5466	5559	6214	6687	7001	7220	7220
MP (kg) (N)[b]	2932		3723		4919	5428	5750	5716	6212	6261	6264	6403	6252
MP (kg) (USA)[c]				4017	4874	5180	5938	6516	6893	7122	7434		
DIM (d) (NL)[a]	308	308	306	304	305	309	311	304	306	311	314	322	325

[a], NRS (1996); [b], NML/Norske Meierier (1996); [c], USDA (1991).

continuing increase in (daily) milk production that has been achieved in the past decades. In dairy cow populations heritabilities of milk production are found around 0.20 to 0.35 (Kennedy, 1984).

3.3.2. Responses in metabolic traits

In early lactation, high producing cows are generally in negative energy balance (i.e. nutrient intake minus requirements) and mobilise body reserves for milk production (Freeman, 1986; Butler and Smith, 1989). Negative energy balance generally reaches its maximum during the first 2 weeks of lactation and recovers at a variable rate (Butler and Smith, 1989). Harrison et al. (1990) found a significantly lower energy balance in 10 selected cows than in 10 non-selected cows at 1, 2, 10, and 11 weeks postpartum, in a 20-year selection experiment for high Predicted Differences in milk yield; 305-day mature equivalent milk yield was 10 814 kg in the high and 6912 kg in the average line.

Body condition scoring, based on a scale from 1 (thin) to 5 (obese), is an accepted subjective method to estimate the degree of fatness to assess body reserves regardless of frame size and body weight (Gallo et al., 1996). Veerkamp et al. (1994) and Gallo et al. (1996) reported an inverse relationship between milk yield and body condition score. Mean body condition score of 219 Holstein cows bred from bulls with highest genetic merit for fat + protein was significantly lower than for 158 non-selected control cows (2.39 vs. 2.54) in a selection experiment of Veerkamp et al. (1994); average 26-week milk yield for the selection and control line was 5540 and 5007 kg, respectively. Loss of body condition score during early lactation was almost twice as high for 401 Holstein cows yielding more than 12,000 kg as for 187 cows yielding less than 6000 kg milk (−0.64 vs. − 0.38 units) (Gallo et al., 1996).

A negative energy balance may be associated with a higher incidence of metabolic disorders, impaired fertility, and other health problems. However, small sample size and the lack of power to detect significant associations may account for controversial results found between authors. Results on relationships between milk production and several metabolical traits are mainly of phenotypic nature since

selection experiments with dairy cows are rare and field data on metabolical traits are practically not available.

Timing, magnitude and recovery rate of negative energy balance may be related to reinitiation of the ovarian activity and interfere with the ability of the hypothalamo-hypophyseal axis to regulate the luteinizing hormone (LH) pulse frequency necessary for ovarian follicular development and ovulation (Butler and Smith, 1989; Canfield and Butler, 1990), and with the ovarian responsiveness to LH signalling (Canfield and Butler, 1991). First ovulation occurred on average 10 days after the most negative energy balance (Butler et al., 1981). The exact way in which negative energy balance may modulate LH secretion is not known. Non-esterified fatty acids provide a potential signal of status of energy balance to neural centres controlling LH secretion (Canfield and Butler, 1991). Failure of early reinitiation of ovarian activity may result in fewer ovulatory cycles before insemination and thus result in a lower conception rate and decreased fertility (Butler and Smith, 1989; Senatore et al., 1996). Harrison et al. (1989) suggest that suppression of oestrus behaviour, rather than the time to initiation of ovarian activity in high-producing Holstein cows may be a factor affecting the interval from parturition to conception.

Barnes et al. (1985) found in a selection experiment similar insulin concentrations, higher mean growth hormone (GH) concentrations and lower mean glucagon concentrations in 18 Holstein cows selected for high milk production compared to 18 cows from a randombred control line. It is suggested that this combination is related to increased conversion of adipose tissue into energy source, reduced lipogenesis, and increased efficiency of lipolysis in the selected line. Average mature equivalent 305-day milk production was 7890 kg in the selection group and 6885 kg in the control group. Bonczek et al. (1988) reported a decreased insulin concentration, an increased somatotropin concentration and unchanged concentrations of prolactin and thyroxine with selection for milk yield: insulin concentrations were 18.80 and 22.50 μIU/ml, and somatotropin concentrations were 4.46 and 3.73 ng/ml in 29 Holstein cows selected for milk yield and 23 unselected cows, respectively. 305-day milk yield averaged 9878 kg for the selection line and 7402 kg for the control

line. Insulin may be a signal to the ovary of metabolic recovery from pregnancy and lactation (Canfield and Butler, 1991).

3.3.3. Responses in reproduction traits

Antagonistic relationships between high milk production and several fertility traits have been observed by several authors (e.g. Hansen et al., 1983; Hoekstra et al., 1994); others, however, found no relationship (e.g. Villa-Godoy et al., 1988; Raheja et al., 1989). Nebel and McGilliard (1993) pointed out in a review about interactions between high milk yield and reproduction, that a trend can be observed in associations found between the two traits. Data collected prior to 1970 show little or no association, whereas an antagonistic phenotypic relationship has been reported more frequently, with increasing milk production, after 1975.

Although few, some selection experiments have been conducted to investigate the consequences of selection for high milk production on reproductive performance; results are given in Table 6. Table 7 gives genetic correlations of 305-day milk production with several fertility traits as analysed by several authors. Genetic correlations of 60-, 80-, and 100-day milk yield with fertility were quite similar in sign and size compared to 305-day milk yield (Berger et al., 1981; Van Arendonk et al., 1989). Results show that in general high producing cows were bred later, showed more days open, had a longer calving interval, a lower rate of non-return at 56 days, and required more services per conception than low producing cows. Ducker and Morant (1984) suggest that both production level and rate of increase in yield in early lactation are associated with reproductive performance.

Long-term experiments in dairy cows have not been conducted due to the long generation interval and high maintenance costs (Kennedy, 1984; Legates and Myers, 1988). Most information is based on field data and thus subjected to aforementioned management policy and possible preferential treatment of high producers. Most data sets contain records that include only cows conceiving and calving normally (Berger et al., 1981). Butler and Smith (1989); Nebel and McGilliard (1993) state that the several interval traits (e.g. days open, calving interval, etc.) are too much dependent on management policy. Estimated

Table 6
Differences between cows selected for high milk yield (HY) and control (C) line cows for postpartum (PP) interval to first ovulation, postpartum interval to first oestrus, postpartum interval to first service, number of inseminations, and days open as analysed by several authors (A)

A	D (yr)	Breed	*N*	Production level		Observations			
				HY	C	Trait	HY	C	
[1]	16	H	625[5]	9100 kg 305-d MP	6883 kg 305-d MP	Differences in trend over years for days open between groups			NS
[2]	20	H	20[6]	10 814 kg 305-d MP	6912 kg 305-d MP	PP interval to 1st ovulation (d)	31	29	NS
						PP interval to 1st oestrus (d)	66	43	**
						Days open (d)	217	74	**
[3]	17	J	1056[5]	6594 kg 1st lact	5528 kg 1st lact	PP interval to 1st oestrus (d)	32	30	NS
						PP interval to 1st service (d)	88	77	***
						Days open (d)	110	99	**
[4, 8]	19	H	187[7]	5454 26-wk MP	4944 26-wk MP	PP interval to 1st oestrus (d)	45	49	NS
						Number of inseminations (d)	1.9	1.8	NS

[1], Legates and Myers (1988); [2], Harrison et al. (1990); [3], Bonczek et al. (1992); [4], McGowan et al. (1996).
[5], Whole selection experiment; [6], last generation; [7], last four calving seasons.
[8], Selection is on genetic merit for kg fat + protein.
D, Duration of selection experiment; H, Holstein; J, Jersey; MP, milk production; N, number of observations.
**, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

Table 7
(a) Genetic correlations between 305-day milk yield (305-MY) and days (from calving) to first insemination (FI), days open (DO), number of services per conception (NS), 56 non-return rate after first insemination (NR56) and calving interval (CI), for parity (PAR) 1, 2 and 3 in dairy cows; (b) Average 305-day milk production (kg) (AP), total number of records (*N*) and breed

a	PAR	305-MY	b	PAR 1		PAR 2		PAR 3	
				AP	*N*	AP	*N*	AP	*N*
FI	1	0.48[a]*, 0.25[b], 0.01[d], 0.22[e], 0.44[f], 0.48[g]	[a]*	6017	–	6837	–	7343	–
	2	0.32[a]*, 0.34[b], 0.23[e]	[b]	–	41 710	–	31 162	–	22 389
	3	0.491*, 0.272, −0.085	[c]	7249	3976				
DO	1	0.62[a]*, 0.37[b], 0.54[c], 0.68[d], 0.64[e]	[d]	4374	5010				
	2	0.15[a]*, 0.43[b], 0.65[e]	[e]	5113	6216	6108	4815	6518	3541
	3	0.18[a]*, 0.39[b], 0.27[e]	[f]	6197	82 659				
NS	1	0.62[a]*, 0.12[b], 0.67[d]	[g]	5765	9163				
	2	0.53[a]*, 0.42[b], 0.46[e]							
	3	0.10[a]*, 0.25[b], 0.36[e]							
NR56	1	−0.26[f]		Breed					
	2	−0.56[e]							
	3	−0.28[f]	[a]	H	[e]	DF			
CI	1	0.66[d], 0.55[f], 0.32[g]	[b]	–	[f]	H/DF			
	2		[c]	H	[g]	H			
	3		[d]	SB					

[a], Berger et al. (1981); [b], Hansen et al. (1983); [c], Seykora and McDaniel (1983); [d], Schneeberger and Hagger (1986); [e], Van Arendonk et al. (1989); [f], Hoekstra et al. (1994); [g], Pryce et al. (1997).
H, Holstein; SB, Swiss Braunvieh; DF, Dutch Friesian.
*, 305-day fat corrected milk yield.

correlations can be affected if high yielding cows are better detected for oestrus, are inseminated later (Berger et al., 1981), are given more opportunities for reinsemination than average and low yielding cows (Raheja et al., 1989; Hoekstra et al., 1994) or are culled less frequently (Fonseca et al., 1983;

Eicker et al., 1996). Conception rate of first breeding or number of breedings are thought to be better indicators of reproductive function (Nebel and McGilliard, 1993; Hoekstra et al., 1994).

3.3.4. Responses in health traits

Much controversy exists about the relationship between production and health traits. Shanks et al. (1978) observed in 171 cows selected for high genetic potential for milk production 9% more cases of digestive disorders (20 and 11%, respectively), 5% more cases of foot rot (9 and 4%, respectively), 14% more cases of skin or skeletal disorders (49 and 35%, respectively), 11% more cases of udder edema (i.e. swelling in the mammary and adjacent tissue), and 2% more lactations affected by mastitis than 187 cows selected for low genetic potential. No differences were found between the groups for respiratory disorders. Cows were subsequently randomly assigned to be bred to bulls with either high or low average Predicted Difference in milk production. Results after the first 6.5 years of selection showed 5% more joint or leg injuries in the selected line (7%) compared to the randombred control line (2%), 3% fewer mammary cuts (0 and 3%, respectively), 13% more total cases of skin or skeletal disorders

(54 and 41%, respectively), and 19% more cases of udder edema. No differences were found between the lines in digestive disorders or respiratory disorders. Wautlet et al. (1990) found in a 23-year selection experiment for high milk yield, comparing 139 selected cows with 172 non-selected control cows, no significant differences in edema, dystocia or retained placenta.

Health registering in the Nordic countries provides valuable data for investigating the epidemiological and genetic background of several health traits. Table 8 gives genetic correlations of 305-day milk production with several health traits as analysed by several authors. These results, although in some cases controversial, suggest that genetic increase in milk yield leads in general to cows higher at risk of mastitis, ketosis and leg problems, but with a lower occurrence of ovarian cyst and displaced abomasum.

As for reproductive disorders, field data on health traits are confounded with herd and management factors: e.g. the ability of the dairyman to recognise a disease, preferential treatment of high producers, different nutritional treatments between herds. Moreover, the underlying assumption about normality of a linear model is not fulfilled in data on threshold characteristics. Disease traits are basically coded as 1

Table 8

(a) Genetic (r_g) and environmental (r_e) correlations between 305-d milk yield (305-MY) and mastitis (MS), ovarian cyst (OC), ketosis (KT), milk fever (MF), displaced abomasum (DA), retained placenta (RP), and leg problems (LP) for parity 1 (P1) or across parities (ACP) in dairy cows; (b) Breed, average 305-d milk production (kg) (AP) and total number of records (N)

a		305-MY			b	Breed	P1		ACP	
		r_g		r_e			AP	N	AP	N
MS	P1	0.21[a], 0.39[d], 0.51[f], 0.37[g], 0.46[h], −0.40[i]		−0.01[g]	a	−	4400	890		
		0.26[b], 0.57[d], 0.18[e], 0.21[i]			b	H			8924	5091
OC	P1	−0.14[g]		0.27[g]	c	FA	−	−	−	70 775
	ACP	−0.01[e], −0.06[g]		0.20[g]	d	FA	−	−	−	70 775
KT	P1	0.30[c], 0.65[f]			e	H			−	11 008
	ACP	0.10[c], 0.26[e], 0.77[g]		0.02[g]	f	−	5017	216 565		
MF	P1				g	H	−	−	−	7416
	ACP	0.27[b], 0.33[e], −0.67[g]		0.15[g]	h	FA	5334	10 152		
DA	P1				i	H	5765	9163	6455	33 732
	ACP	−0.15[e], −0.04[g]		−0.10[g]						
RP	P1									
	ACP	0.26[b], −0.43[e]								
LP	P1	0.24[i]								
	ACP	0.32[e], 0.27[g], 0.29[i]		−0.18[g]						

[a], Bunch et al. (1984); [b], Thompson (1984); [c], Gröhn et al. (1986); [d], Syväjärvi et al. (1986); [e], Lyons et al. (1991); [f], Simianer et al. (1991); [g], Uribe et al. (1995); [h], Pösö and Mäntysaari (1996); [i], Pryce et al. (1997).

H, Holstein; FA, Finnish Ayrshire.

or 0 depending on whether a disease was detected or not. Prediction and estimation procedures based on normality are approximate and may yield poor results (Gröhn et al., 1986). Difficulties in analysing all-or-none traits and the highly multi-factorial nature of diseases may very well account for controversial results found by different authors.

4. A biological explanation for the occurrence of negative genetic correlations

In 1954, Lerner discussed what he called 'genetic homeostasis', the idea that evolution by means of natural selection has developed genotypes that are highly adapted to their environment, since the most adapted phenotypes in a population will predominate. Heterozygosity, stabilised selection and negative genetic correlations between traits will result in intermediate optima for many characteristics in order to maintain this homeostasis. All traits will maintain additive variance which will act as a buffering effect to a wide range of environments, allowing species to genetically change rapidly if the conditions alter.

In 1963, Rendel suggested that genetic correlations may be explained from a situation in which two characters share resources for their development. An increase in resources will result in an increase in both traits and a consequent positive correlation; a limited resource situation, resulting in competition for resources among traits, will result in a negative correlation. Rendel (1963) suggests that selection in order to increase a certain trait may act on both the total amount of resources available and their distribution.

These ideas were worked out further by Goddard and Beilharz (1977) who related total amount of resources available to an animal to fitness in the 'Resource Allocation Theory': fitness is a trait composed of several components, such as 'number of parities' and 'average litter size', which they suggest multiply to give fitness. The resources consumed by these and other processes (maintenance, (re)production, movement, reaction to pathogens and stressors, etc.) they suggest, add to give the total amount of resources consumed (e.g. feed intake, body tissue, etc.), since resources consumed by one process can not be allocated to another process. In a

limited resource situation, fitness will decrease if one of its components increases in combination with an increased allocation of resources to this trait. In this situation, fitness will reach a limit with optimal intermediate values for its components (Beilharz et al., 1993). It is suggested that the process of domestication has increased total amount of resources available to an animal since some resource consuming traits are no longer required, e.g. searching for food, fighting against predators, etc. However, Beilharz et al. (1993) suggest that we must expect domesticated animals to have become again limited by the environment in many situations. Residual Feed Intake (RFI), which is the part of feed intake that is not accounted for by maintenance and (re)production, is suggested as a possible tool to quantify the total amount of resources available to an animal for other processes than maintenance and (re)production, i.e. 'movement', 'reaction to pathogens', 'reaction to stress', etc. in different environments and different metabolical stages of life (Luiting et al., 1995, 1997).

Artificial selection for a particular trait may lead to the situation in which resources are used to the maximum, i.e. no buffer is left to respond adequately to unexpected stresses and challenges. Preferential allocation of resources may occur because the animal may be 'genetically pre-programmed' to allocate a disproportionally large amount of resources to the trait selected for, leaving the animal lacking in ability to respond to other demands. If genetic changes are too radical or sought too rapidly, the population may lack the time required to adapt to the changes imposed on it by selection and the homeostatic balance of the animal is at risk (Dunnington, 1990). The greater the loss of balance, the more negative genetic correlations between production traits and fitness traits will become in order to counteract this loss.

Welfare of an animal is reflected by the success of its attempts to cope with its environment (Broom, 1993), and depends on its physiological ability to respond properly in order to maintain or re-establish its homeostatic state or balance (Siegel, 1995). Any stimulus that challenges homeostasis can be viewed as a stressor, and changes in biological function occur as the animal attempts to respond to the stressor. Alterations in physiological systems to

maintain homeostatic balance will divert resources from the biological functions that occur prior to the stress, which may lead to the development of pathology, e.g. increased susceptibility to disease, impaired reproduction or inefficient metabolism, and thus impaired animal welfare (Moberg, 1985, 1987; Newman, 1994).

5. Discussion and conclusions

The examples presented in this review show that, apart from a highly favourable increase in production, present-day selection for high production efficiency in livestock species in many cases has been accompanied by undesirable side effects for several physiological, immunological and reproduction traits and consequently for animal welfare. Although the continuous increase in production levels suggests a continuous positive selection response for the traits under selection in commercial livestock production, and *desirable* correlated responses to selection are likely to exist as well, it is expected that with ongoing selection for high production efficiency only, the occurrence and magnitude of undesirable side effects will increase.

The most striking examples of undesirable correlated responses are found in broiler chickens with an increasing incidence of heart failure syndrome and leg problems. In poultry breeding programs selection has been almost for one trait only, i.e. body weight at a certain age, with a high selection intensity and a short generation interval. In species like cattle and pigs, where the results are obviously more controversial, selection has been less intensive, for more traits and during fewer generations. Moreover, especially in dairy cattle, undesirable side effects may be camouflaged because of the multi-factorial nature of most problems, which does not, however, mean that genetic relationships between production traits and undesirable traits are absent. Since many literature references do show the presence of undesirable side-effects of selection in dairy cattle, it may be concluded that selection has indeed made also these animals more sensitive to metabolic, reproduction and health problems.

Future application of DNA-technology and modern reproduction technologies may increase production faster than at present. This will, however, also increase the speed of expression of detrimental antagonistic relationships with selection for high production efficiency. In this perspective, the undesirable effects found in broilers may be considered as a forerunner for similar problems to be expected in other species under selection. It is important to avoid this for several reasons: (1) there is increasing consciousness among people of the intensive nature of animal production systems and social resistance against some production systems will increase if animal health and welfare become more at risk, (2) veterinary costs and costs of replacing animals will further increase, (3) if breeding programs should be altered it may take five to ten years before genetic trends in commercial livestock are really changed.

In an evolutionary perspective, in nature those animals with high fitness have a higher contribution of alleles to the population in future generations than animals with low fitness. Consequently, alleles related to high fitness (i.e. health, reproduction, longevity, etc.) replace alleles related to low fitness. According to the Resource Allocation Theory of Beilharz et al. (1993), when (internal and/or external) resources are limited, a compromise has to be found how to partition available resources among traits. Assuming that in nature alleles related to highest fitness predominate, the optimal partitioning of resources in nature is accomplished by allocating intermediate proportions to fitness traits which will maximise overall fitness.

With artificial selection, however, the 'optimal situation' is being redefined towards high production. Moreover, fitness does not necessarily have to be as defined in nature, e.g. long reproductive life may not be necessary, but animals have to be (reasonably) healthy and reproductive. The theory implies that once a breeding goal has been defined, there is an optimum to what can be accomplished in a given, resource limited, environment. Increasing production by selection beyond this optimum will be compromised because the environment is not able to support the essential increase in resources required, resulting in a *deviation* from the optimum (Beilharz, 1998). When a population is genetically driven towards high production, and thus allocating a higher proportion of resources to this trait, less resources will be left to respond adequately to other demands, like coping

with (unexpected) stressors; i.e. the buffer capacity is affected. In this situation it is most likely that those traits not defined in the breeding goal will be the first ones from which resources will be diverted towards increased production.

The theory implies that a set of alleles in a given environment, maximally supporting the breeding goal by optimally allocating available resources to the traits included, will not maximally support the breeding goal in a different environment. High producing Western dairy breeds are not able to fully express their potentially high production level while maintaining the level of health and reproduction when they have to deal with heat stress, diseases and limited nutrient supply in the tropics, as is well recognised (e.g. Syrstad, 1989; Menendez Buxadera and Dempfle, 1997). Consequences will be less pronounced for differences only in management systems, food composition, etc.

When the Resource Allocation Theory (Beilharz et al., 1993) holds, and future research into the quantitative aspects of resource allocation is desired, negative side effects of selection may be predicted and thus prevented. Modification of the environment to increase the amount of resources available to an animal, e.g. by increasing the energy amount of feedstuffs or by reducing environmental stress (e.g. Specific Pathogen Free environments), may prevent negative side effects of selection or even allow for improved output levels. However, possibilities to change the environment are limited and costly, and the population may become more dependent on the specific environment. Furthermore, selection for increased feed intake capacity may increase the resource situation. Efficiency parameters have to be handled with care: although increasing net efficiency of a specific trait may improve the resource situation, increasing feed efficiency for production may be (partly) at the cost of resources left to respond to stressors (e.g. maintenance requirements) and may thus have the opposite effect.

A more fundamental solution is to redefine the breeding goal into a broader perspective. It means breeding animals with a long economical (re)productive life at a production level that is economical (i.e. production in relation to veterinary costs, etc.) without giving any signs of disturbed welfare. Those traits will have to be closely defined. Livestock breeders will have to be satisfied with a slower increase in (re)production.

Moreover, animals will have to be selected preferably within specific environments (e.g. regions, management systems) for selection to be most effective, since different environments have different optima. Mathematically accounting for differences in environmental conditions may only result in a further deviation from the optimum when animals end up in an environment that can not support the required amount of resources to fully express the genetic potential.

Finally, when the optimum is reached, i.e. the breeding goal is maximally supported, production can be further increased only when the resource situation (internal and/or external) is improved or the breeding goal is redefined.

Although the economic importance of genetic changes in production traits is clear, relatively little research has been directed to the biological aspects of selection. Animal breeding scientists have concentrated mainly on the technical aspects of breeding value and genetic parameter estimation. Without knowledge about the underlying physiological processes on which genetic selection acts, cumulative and permanent genetic improvement through selection is essentially a black box technique. Speeding up genetic increase, e.g. with application of modern reproduction techniques and DNA-technology, in a biological system that is not well understood is very likely to lead to unfavourable and improperly understood side effects, if not to disorders (Luiting, 1993). Knowledge of biological backgrounds, including typing of genes and identifying their specific role within physiology, will offer the opportunity to understand, anticipate and prevent negative side effects of selection.

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