

## Genetics of lactation persistency

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### Abstract

Lactation persistency, often simply called persistency, in general can be defined as the ability to maintain yields during the lactation. Persistency has an impact on food costs, health, and fertility. Of these three components affected by persistency, the impact of persistency on health, i.e. metabolic stress of the cow leading to health problems, may be most important nowadays. Numerous suggestions for criteria of persistency exist. Often simple ratios of part-lactation yields, e.g. the ratio of yield in the first and last 100 days of lactation, have been used. New approaches have used results from the application of random regression test day models developed for the genetic evaluation of yield traits. Many studies unfortunately have neglected the effect of gestation on persistency but acknowledged that an improved persistency should lead to an improved reproductive performance. Both relationships should be considered in genetic analyses and recommendations for improvement of management decisions. Today the correct description of persistency plays a prominent rôle to obtain correct genetic evaluations based on test day yields. But, although apparently trivial, a direct genetic analysis of lactation persistency and even more an inclusion of this trait into selection programmes clearly is a complicated task. A reason for this, amongst others, is that management strategies for feeding during the lactation and handling of the reproductive performance that are most often not recorded, are likely to mask the real persistency. Future studies on the genetics of persistency should also seek a strong interaction of geneticists and physiologists as persistency is fundamentally confounded with the problem of metabolic stress. Today, a recommendation of the inclusion of persistency in selection programmes appears to be premature and more studies, e.g. on the association of persistency with longevity, could aid in this process.

### Introduction

Lactation persistency, often simply called persistency, in general can be defined as the ability to maintain a more or less constant yield throughout of the lactation. The lactation of a cow is more persistent if, for the same total yield, the peak yield is lower and the lactation curve is flatter. Persistency is a trait of economic importance because of its impact on food costs, health, and fertility (Dekkers *et al.*, 1998). Of these three components that are affected by persistency, the impact on health, i.e. metabolic stress of the cow leading to health problems, may be more important than its impact on food costs. Food costs can be derived from calculations in which for more persistent cows feeding of concentrates can be replaced partly by roughage thus reducing food costs. Economic calculations have been undertaken by Sölkner and Fuchs (1987), Gengler (1995) and Dekkers *et al.* (1998). However, today differences between costs for concentrates and roughage are more and more marginal. The avoidance of metabolic stress within the first trimester of lactation is known to improve reproductive performance and thus also reduces costs for reproduction, although this reduction may vary considerably under different management policies and production levels. According to Dekkers *et al.* (1998) the economic value of persistency should be derived independently from the production yield since lactation yield is already included in the aggregate genotype. Gengler (1996) distinguished between apparent and real persistency that is defined considering total yield as constant. Following this, a prime requirement for a criterion of persistency should be that the measurement is independent from lactation yield. However, numerous suggestions for criteria of persistency can be found in the literature and only very few studies deal with the problem of a dependency of the criterion on (lactation) yield. Genetically, the independence of a specific criterion should not be evaluated according to the phenotypic relationship but rather by its genetic relationship, i.e. genetic correlation, between the two measurements. This has been emphasized by Jamrozik *et al.* (1998).

### Criteria of persistency

The criteria found in the literature may be separated into four groups. The first group contains criteria derived from mathematical models describing the lactation curve. The second group are measures based on ratios between total, partial, maximum or other yields. A third group is formed by criteria measuring the variation of yields in the course of the lactation. A fourth relatively new group has been suggested based on the application of random regression test day models.

#### *Criteria derived from lactation curve models*

Numerous mathematical models to fit lactation curves have been developed, for a review see Masselin *et al.* (1987) and later literature reviews by Olori (1997) and Guo (1998). When developing mathematical functions describing the lactation curve, the common aim was to predict test day, or accumulated (part-) lactation yields, or to describe the influence of environmental effects on the shape of lactation curves. Recently there has been an increasing interest in lactation curve models, largely triggered by the proposal of a one-step test day model for the genetic evaluation of animals in the study of Ptak and Schaeffer (1993). In a one-step test day model, observations (test day yields) within a lactation are treated as repeated measurements, the shape of the lactation curve is accounted for by an appropriate function (lactation curve model) which thus could be called a sub-model within the animal repeatability model (Swalve, 1995a and 1998).

As a by-product, some mathematical functions can be used to define criteria of persistency. The most simple model for a lactation curve would be a linear regression of test day yields on days in milk. Although obviously not really appropriate as a lactation curve function since lactation curves for yield traits consist, at least clearly distinguishable for milk, of an ascending phase between calving and peak yield, a more or less constant production around peak yield and a descending part after peak yield (Gengler, 1995), the regression coefficient could be viewed as a criterion of persistency. This was proposed by Madsen (1975) and Gravert and Baptist (1976). The first model that was able to describe the three phases within a lactation was proposed by Wood (1967). It is defined as

$$y_t = a t^b e^{-ct}$$

In this model,  $a$ ,  $b$ , and  $c$  are parameters to be estimated and linked to the ascending phase, the peak, and the descending phase of the lactation, respectively. The stage of lactation (weeks, days) is defined by  $t$ . The parameters are readily estimated after a natural logarithmic transformation that

transforms this model to a completely linear one. From this model, Wood (1967) proposed the parameter  $S$ , where

$$S = c^{-(b+1)}$$

as a criterion of persistency.

Several authors have used this parameter when analysing lactation persistency (e.g. Madsen, 1975; Shanks *et al.*, 1981; Leukkunen, 1985; Ferris *et al.*, 1985).

Grossman and Koops (1988) developed a multiphasic lactation curve function. In their model, persistency may be defined as the duration of the second phase of the lactation.

#### *Criteria based on ratios of yields*

Measures based on ratios between total, partial, maximum or other yields have been discussed since the work of Sanders (1930). He defined persistency as the ratio between mean and peak yield. Madsen (1975) used the ratio of total yield during lactation divided by peak yield. Similarly, Lean *et al.* (1989) proposed to use the ratio of 305-day lactation yield divided by peak yield multiplied by 305 days. In this sense, higher values of the criterion are associated with a higher persistency. Contrary to this definition, Leukkunen (1985), Sölkner and Fuchs (1987) and Swalve (1994a, b and 1995b) used the ratio of peak yield divided by the average yield during lactation or parts of the lactation (e.g. first 200 days). Thus, in these studies, higher values of the criterion are indicators of lower persistency.

Johannsson and Hansson (1940) introduced ratios of partial yields, namely the ratio of production in the second 100 days to that of the first 100 days and analogously the ratio of the last to the first trimester of lactation. Mainly due to their ease of computation and their obvious attempt to compare ascending and descending phases of the lactation, these measurements became very popular and many modifications can be found in the literature. Amongst others, ratios of this type and their modifications have been used by Madsen (1975), Danell (1982), Leukkunen (1985), Sölkner and Fuchs (1987), Kandzi and Glodek (1990) and Swalve (1994a, b and 1995b). For these types of criteria, higher values always indicate higher persistency. Depending on the parts of the lactation reflected in the ratios, either production in the third and first, or second and first, or third and second trimester, the criteria often are denoted as P31, P21, and P32.

#### *Criteria associated with the variation of test day yields*

In its simplest form the standard deviation of test day yields during the lactation is used (Sölkner and

Fuchs, 1987). Sökner and Fuchs emphasize that this criterion not only attempts to measure persistency as commonly defined, but also considers variations of test day yields due to undesirable oscillations of the lactation curve. Furthermore, the distribution of this criterion is closer to a normal one than for other measurements of persistency. Gengler (1996), however, pointed out that across all cows analysed, official test days are not on the same days. Specific lactations could vary considerably from ideal sampling intervals. Furthermore, the standard deviation of lactation yields clearly is not independent of the total or average yield per day in the lactation. Modifications to account for this have been proposed by Gengler *et al.* (1995). They used a criterion called yield variation measuring the variation of accumulated part-lactation yields and combining these values into an index. Gengler (1995) pointed to the fact that a square-root transformation of yield variation provides a persistency parameter that has a near perfect normal distribution.

#### *Criteria derived from random regression test day models*

As an extension of the suggestion by Ptak and Schaeffer (1993) to model test day records in a one-step test day repeatability model, Schaeffer and Dekkers (1994) proposed the use of random regression models. In random regression test day models the repeated measurements (test day yields) within a lactation are modelled partly by fixed regression coefficients, often nested in appropriate sub groups of the data (e.g. calving age and season) and partly by random regression coefficients associated with the animal's genetic effect and the permanent environmental effect, thus allowing for a covariance structure among the coefficients (Jamrozik *et al.*, 1997a). Random regression models are specific formulations of the concept of covariance functions developed for the analysis of repeated measurements data (Meyer and Hill, 1997; Meyer, 1998). According to Hill (1998) such models will completely replace models considering fixed time points for the repeated measurements thus circumventing the problem of a decision whether measurements are 'repeated' or 'separate' traits with a specific covariance structure among them.

In random regression test day models, the genetic variance and 'genetic yields' for each single day of the lactation can be estimated and used to define suitable criteria of persistency. Due to this flexibility, various criteria of persistency can be derived from genetic evaluations under random regression test day models analogous to the definition of phenotypic measurements as done by the criteria in the first three groups (Dekkers *et al.*, 1996). The difference from the traditional measurements lies in

the use of the 'genetic yields'. Jamrozik *et al.* (1998) proposed to measure the average slope of the animal's lactation curve between days 60 and 280 of the lactation.

## **Non-genetic factors affecting persistency**

In general, mixed models for the analysis of genetic and environmental influences on persistency are similar to models studying yield traits. Thus a dominant effect is the herd effect comprising differences among herds with respect to feeding and management practises. Other effects are parity, age at calving, season of calving and pregnancy.

#### *Parity*

First lactations in general have been found to be more persistent than later lactations (e.g. Shanks *et al.*, 1981; Danell, 1982; Keown *et al.*, 1986; Sökner and Fuchs, 1987). Hence, if analysed jointly, this effect should be considered in the model. An explanation of this effect could be that the generally higher performance in later lactations (first lactation heifers are still growing) is leading to sharper peaks of the lactation curve that obviously are associated with lower persistencies (Gengler, 1990).

#### *Age at calving*

Influences of the age at calving within parity have been found to be small (Danell, 1982; Grossman *et al.*, 1986). A slight trend towards a reduction in persistency with increasing age is observed (Gengler, 1990). This may be attributed to the same relationship between persistency and yield as discussed for the effect of parity. Within certain limits, it is well known that yields increase with age at calving. From this, a more developed mammary gland of an older animal should also lead to sharper peaks of the lactation curve.

#### *Season of calving*

In many studies a pronounced effect of the season of calving on persistency has been found (e.g. Danell, 1982; Ferris *et al.*, 1985; Grossman *et al.*, 1986; Sökner and Fuchs, 1987; Gengler, 1990). However, different seasons have been found that have a positive effect on persistency. This finding should be attributed to differences in regions across the world and the specific management practices found in them. In regions with distinct climatic seasons and especially in pasture-based systems a strong seasonal effect is expected, while in regions with less climatic variations and operating in-door systems this effect may be negligible. Furthermore, the criteria used play an important role. Criteria covering only specific parts of the lactation as opposed to the entire

**Table 1** Estimates of heritabilities of 'traditional' (or slightly modified, detailed explanations are in the text) criteria of milk yield persistency and the genetic correlation with first lactation yield from the literature since 1980 (S = persistency as defined by Wood, 1967; P21 and P31 are ratios of production in second divided by first and third divided by first trimester of lactation, respectively)

Author	Breed	Method of estimation†	Estimates of heritabilities				Estimates of genetic correlations				
			S	P21	P31	Total/peak or Peak/total	S	P21	P31	Total/peak or Peak total‡	
Shanks <i>et al.</i> , 1981	Holstein	H-III	0.02								
Schneeberger, 1981	Brown Swiss	H-III		0.22	0.29				0.16	0.11	
Ferris <i>et al.</i> , 1985	Holstein	REML-SM	0.04					0.52			
Danell, 1982	SLB (Holstein)	H-III§		0.14					0.55		
				0.11							
Leukkunen, 1985	Ayrshire	H-III	0.08	0.11		0.11	0.00		0.17		-0.17
Batra <i>et al.</i> , 1987	Holstein	REML-SM	0.21				0.56				
Sölkner and Fuchs, 1987	Simmental	REML-SM		0.14	0.19	0.17		0.50	0.48		-0.53
Kandzi and Glodek, 1990	Holstein	H-III		0.11	0.11			0.27	0.18		
Swalve, 1995b	Holstein	REML-AM§			0.11	0.15			0.56		-0.53
					0.11	0.15			0.52		-0.57
Gengler, 1995	Holstein	REML-AM¶	0.06				0.54				
Gengler <i>et al.</i> , 1995	Holstein	REML-SM		0.12	0.11	0.08		0.65	0.51		-0.63

† H-III: Henderson's method III; REML: restricted maximum likelihood; SM: sire model; AM: animal model.

‡ Correlations expressed as if parameter was peak total.

§ First row: no correction for milk yield; second row: correction for milk yield.

|| Two-step analysis with pre-corrections and simple REML-SM afterwards; pre-corrections included lactation yield.

¶ Logarithm of S.

lactation will lead to different results with respect to seasonal differences (Sölkner and Fuchs, 1987).

#### Gestation

While persistency may be viewed as a factor influencing reproductive performance (Dekkers *et al.*, 1998), i.e. the chance to get the cow pregnant again, the status of pregnancy (not-pregnant, pregnancy at successive stages) in turn affects persistency. Pregnancy status can be accounted for by including in the model number of days open (e.g. Schneeberger, 1981; Danell, 1982; Grossman *et al.*, 1986; Sölkner and Fuchs, 1987), days in calf (Keown *et al.*, 1986) or calving interval (Gengler, 1990). While some studies did not find any influence of gestation on persistency (e.g. Danell, 1982), a majority of authors did conclude that gestation does indeed have a depressing effect on persistency (e.g. Sölkner and Fuchs, 1987; Gengler, 1990). The reason for this inconsistency in the literature may again be attributable to large differences among the populations and production levels studied. Under a high production level, as studied by Lean *et al.* (1989), an interesting relationship exists between persistency and reproductive performance. Lean *et al.* report that cows with high persistency had lower reproductive performance (percentage of pregnant cows after two breedings). This is quite contrary to the assumption of Dekkers *et al.* (1998) that a high persistency should have a positive influence on

reproductive performance. The reason behind this phenomenon is that cows with a high reproductive performance, i.e. cows which conceive rapidly after calving, are subject to higher metabolic load since the beginning of the new pregnancy almost coincides with the time of the peak yield. Peak yields generally are expected to occur at about 50 to 60 days after calving. A high metabolic load obviously has a depressing effect on persistency. Thus, cows with a superior reproductive performance show a low persistency and *vice versa*. Unfortunately, not many authors have considered gestation in their models of analysis. This is largely due to the apparent problems in collecting suitable data. Even in recent studies this effect is often neglected (e.g. Jamrozik *et al.*, 1998).

## Genetic parameters for persistency

### Heritabilities

Estimates of heritabilities using the 'traditional' criteria as described in groups one to three reported in the literature range from under 0.05 to over 0.30 (Gengler, 1996). In Table 1 estimates for first lactation milk yield persistencies are presented. The presentation is restricted to estimates found in the literature since 1980 and to criteria of persistency that have been used by several authors. As explained above, the fourth criterion exists in different variants that differ by taking peak yield in the numerator or

denominator of the ratio. In the studies by Leukkunen (1985), Sölkner and Fuchs (1987) and Swalve (1994a,b and 1995b) always the version peak/total was used. Thus, higher values for the criterion are associated with lower persistency.

With but very few exceptions, the results are remarkably similar across all methods and models used, across all populations studied, and across all criteria. The criterion *S* derived from Wood's lactation curve function (Wood, 1967) tends to exhibit slightly lower heritabilities in four out of five studies listed.

Estimates for fat and protein persistency have only been studied by fewer authors (e.g. Schneeberger, 1981; Danell, 1982; Kandzi and Glodek, 1990; Swalve, 1994a and 1995b; Gengler, 1995; Jamrozik *et al.*, 1998). A slight tendency was observed of highest estimates for milk yield as compared with fat and protein. Since the heritabilities for criteria of persistency certainly are different from zero, a selection for persistency, if desired, seems to be feasible.

Based on results from a random regression test day model, Jamrozik *et al.* (1998) reported heritabilities at the upper bound of the range as given above. It may be hypothesized that for this study, neglecting the status of pregnancy may have led to an overestimation of the heritabilities. In their study, the trends in estimates for milk, fat and protein resemble the finding discussed earlier: Highest estimates are found for milk yield persistencies.

#### *Genetic correlations among criteria of persistency for identical traits*

Genetic correlations between different persistency traits have only rarely been reported. Schneeberger (1981) found a correlation between P21 and P31 of around 0.90 for milk and fat persistencies. Sölkner and Fuchs (1987) also presented a correlation of 0.89 for P21 and P31 and even higher values (with a negative sign due to their definition of the trait) between P21/P31 and peak/total. Interestingly, these authors also found a very strong negative correlation (close to -1.0 due to their definitions of persistency criteria) between P21/P31 and criteria measuring the standard deviation of test day yields in the course of the lactation. In conclusion, genetic relationships between different criteria of persistency appear to be very strong.

#### *Genetic correlations among persistency yield traits*

Genetic correlations between persistencies for milk, fat, and protein yield also are scarcely found in the literature. Most studies analysed persistency trait by trait and not jointly in a multiple trait model. The results from Gengler (1995) and Jamrozik *et al.* (1998)

suggest that genetic correlations between milk and fat persistency and between milk and protein persistency are around 0.80 and 0.90, respectively. This reflects the genetic correlations among the yield traits. Generally, the genetic relationship between milk and protein yield has been found to be stronger than that between milk and fat yield.

#### *Genetic correlations between subsequent lactations*

The same two studies (Gengler, 1995; Jamrozik *et al.*, 1998) present a very problematic finding with respect to a possible selection for improved persistency: the repeatability of persistency in successive (first, second, third) lactations is fairly low. Jamrozik *et al.* (1998) reported genetic correlations around 0.30 between persistencies for identical traits in successive lactations. It is very difficult to understand why persistency in successive lactations should be separate traits and be influenced by different genes.

#### *Genetic correlations with yield*

The crucial question, however, is the relationship with yield traits. Using the classical measurements of persistency, i.e. groups 1 to 2 as defined above, often positive genetic correlations in a sense of the expected correlated response when selecting for yield traits are found (Table 1). For group 3 (persistency measured as the variation of test day yields) negative genetic correlations again in a sense of the expected correlated response (around 0.40) with yield have been reported (Sölkner and Fuchs, 1987; Swalve, 1995b). Higher yields thus seem to be associated with a higher variation in test day yields, a finding, that at least partly is attributable to a scale effect. The negative correlation was lower (-0.09) using yield variation (Gengler *et al.*, 1995). From the correlations of the criteria in groups 1 and 2 many authors (e.g. Danell, 1982; Swalve, 1995b) have concluded that persistency is not expected to deteriorate when selecting for higher yields. This is also true when only parts of the lactation are used as selection criteria (Swalve, 1995b) with the exception for very early parts in the course of the lactation, i.e. yield on test days 1 to 2 or 1 to 3 (Danell, 1982; Kandzi and Glodek, 1990).

Jamrozik *et al.* (1998) advocate their definition based on the application of a random regression test day model since the trait genetically seems to be uncorrelated with lactation yield. The argument behind this is given by Dekkers *et al.* (1998) and Jamrozik *et al.* (1998). Since yield traits are already included in the breeding goal, the value of a selection for increased persistency should be derived from its impact on costs for health, reproduction, and food and the impact on returns from milk for a given 305-day production.

## Genetic evaluation of persistency

Few countries are evaluating persistency on a routine base yet. Austria is an exception using an approach derived from the study by Sölkner and Fuchs (1987). But recently VanRaden (1998) pointed out that including persistency in a bivariate analysis with yield would provide many of the benefits of a regular test day model. Similar suggestions were made previously by Gengler (1995) who pointed out that the best way to evaluate persistency would be to do it jointly with yield. Another way to evaluate persistency could be based on the use of random regression models (Schaeffer and Dekkers, 1994) and will be implemented in the Canadian random regression test day model that is due to be introduced in 1999.

## Discussion

Studies on the genetic background of lactation persistency first of all have to tackle the problem of a definition of persistency. The statement that a flatter lactation curve *per se* is advantageous is a clear oversimplification of the problems that have to be solved. Jamrozik *et al.* (1997b) state that it is unclear whether a selection for improved persistency is desirable. The general aim in dairy production is a healthy cow, capable of high production and a sufficient reproductive performance. During the time of peak yield, the desired maintenance of high yields, and conception, i.e. within a period of about 60 to 120 days in milk, cows are subject to a high metabolic load. This period often is called the critical part of the lactation. The problem can be approached in various ways. First, management practices have to be in accordance with the performance of the cow. This not only applies to feeding of cows but also to other management decisions. An important effect is the number of days open. This is clearly a predominantly management based decision. Higher yields have to be associated with longer calving intervals. This is not only true from a biological point of view but also economically justified since the dominant share of the income of dairy farmers stems from selling milk and not from the production of calves even although needed for replacements. Bio-economic models that account for this should be used. The very recent study by Dekkers *et al.* (1998) is an example for this approach.

Problems arise when the optimal form of the bio-economic model has to be found. An example is the oversimplification by Dekkers *et al.* (1998) who describe the relationship between persistency and reproductive performance as a one-way link. Persistency is expected to affect reproductive performance before the cow is inseminated successfully. Cows of higher persistency have flatter

lactation curves leading to lower metabolic stress and thus should exhibit a superior reproductive performance. However, as already pointed out, after the successful insemination, gestation affects persistency. This leads to two conclusions. First, studies analysing the genetics of lactation persistency should always account for reproductive performance, i.e. the influence of gestation. Secondly, bio-economic models for optimal management strategies have to consider the two-fold relationship between persistency and reproductive performance. When applied correctly, such models should lead to recommendations for optimal management strategies.

Genetically, the goal should be that the cow that is capable of coping with metabolic stress from the two sources: production and reproductive performance. In this sense, a cow with a completely flat lactation curve may not be the most desirable animal. Rather, a cow with a less pronounced lactation peak and a prolonged maintenance of high yields should be sought.

Criteria derived from random regression test day models have a clear advantage over other approaches. They are based on 'genetic yields' per day and can be altered and compared with respect to their properties in a very flexible way. Criteria are needed that relate to the critical part of the lactation. Their genetic background should be evaluated and further analyses will be needed that study the relationship with other traits related to metabolic stress, e.g. food intake capacity and food conversion. These traits, however, have the intrinsic defect that they are difficult to measure in cows and under practical conditions. New physiological traits may be needed.

In a first step, the relationship between persistency and longevity needs to be analysed. Until now, little has been known in this field. Reents *et al.* (1996) presented correlations between estimated breeding values of bulls for persistency and the percentage of disposals of their daughters during the first lactation. Although these correlations were fairly low, a trend to increased survival rates of daughters of bulls with a higher persistency estimated breeding value (EBV) could be observed. Today, sophisticated methods for a genetic analysis of longevity in dairy cows exist (e.g. Ducrocq and Sölkner, 1998). Until now only few results were known, relating EBVs from survival analysis to persistency. Druet (1998), using several Austrian breeds, estimated genetic covariances between persistency and survival on deregressed EBVs using the multiple across-country evaluation (Schaeffer, 1994) EM-REML approach developed by Sigurdson *et al.* (1996). He found that in most dairy or dual-purpose breeds the correlations were around

0.20 to 0.30 between persistency and survival. Combined with other advances in the genetics of dairy production, i.e. random regression models or covariance functions, studies applying both techniques should give some insight in the question whether persistency should be altered by selection.

Covariance functions could also be used for the analysis of persistency in subsequent lactations. Gengler (1996) and even more Jamrozik *et al.* (1998) have pointed out that the genetic relationship between persistency in successive lactations is rather weak. This finding is not easy to explain and could be an artefact. Another explanation for this phenomenon could be that later lactations are selected samples of the data since only cows capable of sustaining metabolic stress remain in the herd. Until now, the models used have not been able to account for this type of selection. In the case of the study by Jamrozik *et al.* (1998) also the neglect of the effect of gestation could have contributed to this finding.

## Conclusion

Today the correct description of persistency plays a prominent rôle to obtain correct genetic evaluations based on test day yields. But, although apparently trivial, a genetic analysis of lactation persistency and even more an inclusion of this trait into selection programmes is clearly a complicated task. The reason for this, amongst others, is that persistency is affected by management strategies that are often not recorded in the data available. Management strategies for feeding in the course of the lactation and policies for the handling of the reproductive performance are likely to mask the real persistency that may be desirable as a trait for selection. Future studies on the genetics of persistency should also seek a strong interaction of geneticists and physiologists and view the problem of persistency as fundamentally confounded with the problem of metabolic stress. A recommendation of the inclusion of persistency in selection programmes at the current status of knowledge appears to be premature. Genetic studies on the association of persistency with longevity furthermore could aid in this process.

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