

REQUIREMENTS AND USES OF GENETIC EVALUATIONS FOR CONFORMATION AND HERD LIFE

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SUMMARY

Genetic aspects of herd life and conformation traits and their role in genetic improvement programs for dairy cattle are addressed. Based on the nature of relationships between production and herd life, survival ability (involuntary culling) rather than herd life should be included in the breeding goal. The economic value of survival ability is around 40% relative to production. Alternative definitions of recorded herd life traits are discussed, as well as their genetic parameters and properties of associated methods for genetic evaluation. Potential biases in genetic parameters and the associated benefit of adjusting herd life for production are discussed. Methods for recording conformation traits and their genetic parameters and relationships with herd life are reviewed. Finally, incorporation of genetic evaluations for herd life and conformation in selection programs is discussed. It is concluded that direct or indirect (based on conformation traits) genetic evaluations for herd life can aid genetic improvement for overall economic merit. However, genetic evaluations for HL should be considered an intermediate step towards development of selection strategies based on genetic evaluations for fertility traits and resistance to disease.

INTRODUCTION

Herd life (HL) or longevity has long been acknowledged as a trait of major economic importance in dairy cattle. Direct selection for longevity is hampered by the time it takes to complete herd life. As a result, conformation traits have been used for many decades as indirect selection criteria, but frequently without extensive scientific background on genetic relationships. In the past decade, increasing research emphasis has been placed on quantifying genetic relationships between conformation traits and HL and on possibilities for selection for HL based on direct genetic evaluations.

Objectives of this paper are to consider the role of HL and conformation traits in current breeding programs for dairy cattle and to consider data and methods for genetic evaluation and selection. The aim is not to give an exhaustive review of all published material, but is to identify opportunities and problems. Although conformation traits may be related to other traits of interest (e.g., dystocia, mastitis, fertility, laminitis, and feed intake and efficiency), HL will be the main focus herein.

A STRUCTURAL MODEL FOR HERD LIFE

Herd life is determined by individual culling decisions of producers. Most culling decisions are not forced but economic in nature (Van Arendonk, 1986); ideally, a cow is culled because more profit is expected from the replacement than from keeping the current cow. However in practise many other, often subjective, factors may play a role. In general, reasons for culling can be separated into voluntary (primarily production) and involuntary reasons (primarily health and fertility). Based on this classification, the following structural model for HL will be used, in which a cow's phenotype for HL (P_{HL}) is a function of production (P_V), through voluntary culling, and of survival ability (P_S), which includes all other factors affecting HL. P_S is not observed directly, but could in turn be written as a function of health and fertility traits. The following linear model will be used for illustrative purposes, although more complete models are available (e.g. Robertson, 1966): $P_{HL} = m_V P_V + m_S P_S$. In this model (see Figure 1, from Dekkers, 1993), m_V and m_S are standard partial regression coefficients of HL on production and survival ability (all variables standardized). Production affects HL directly through m_V , which represents voluntary culling, and indirectly through its correlations with survival ability.

Relationships between production and herd life. In the model, P_V represents the criterion a producer uses to incorporate production into a culling decision. In a study on optimal culling and insemination

strategies, Van Arendonk and Dijkhuizen (1985) found that optimum decision rules for voluntary culling were almost independent of herd average production, when rules were expressed based on production relative to herd average. This implies that the absolute level of production below which culling is optimum increases with herd average. These results follow economic replacement principles, in which profits of the current cow and its replacement are compared, and seem to hold in practise; average HL has been stable or declined, while absolute production has increased dramatically over the past decades (Nieuwhof et al., 1989). In the model, the effect of production on HL is assumed linear for simplicity. Field data (e.g., Allaire, 1968; Ducrocq et al., 1988; Dekkers et al., 1994) and theoretical models (Van Arendonk and Dijkhuizen, 1985) indicate nonlinear relationships, with asymptotes at low and high production.

Use of relative rather than absolute production as criterion for voluntary culling has important implications for the interpretation of the positive phenotypic and genetic correlations between production and HL that are found in many studies (e.g., Strandberg, 1985). Culling on relative production induces a positive correlation between HL and production within herds. However, this correlation does not hold across herds or generations that differ in level of production: herds with a higher average production do not necessarily have a higher average HL. Also, genetic improvement of production does not translate into a correlated positive response in HL. The nature of the genetic relationship between production and HL can be explained by a negative covariance between genotype and environment for HL (M.E. Goddard, unpublished): as genetic merit for HL improves with selection for production, the environment for HL becomes more stringent through an increase in the level of absolute production below which culling takes place.

THE ROLE OF HERD LIFE AND CONFORMATION IN THE BREEDING GOAL

Herd Life Herd life is a complex trait, which combines traits related to production, health, fertility, and workability. Ideally, these traits should be specified separately in the breeding goal (Rogers, 1994), which would make HL redundant. Formulating the breeding goal in terms of HL is an alternative that is easier to implement because it requires fewer economic and genetic parameters. However, this approach does reduce completeness of the breeding goal; Allaire and Keller (1990) estimated that a breeding goal of production and HL would leave 15% of genetic differences in economic merit unaccounted for. The impact on efficiency of the resulting selection index may, however, be small because phenotypic data on health and fertility traits is often not readily available.

Conform the previous section, strategies for improvement of HL should focus on improving survival ability (A_s in Figure 1) (Van Arendonk, 1986). Therefore, survival ability rather than HL should be included in the breeding goal. Economic benefits from improving survival ability result from lower replacement costs, lower health costs, an increased proportion of cows in higher production ages, and increased opportunities for voluntary culling (Van Arendonk and Dijkhuizen, 1985). On a genetic SD basis, estimates of the economic value of survival ability relative to production range from 20 to 60%, with most estimates around 40% (Burnside et al., 1984; Rogers et al. 1988; Allaire and Gibson, 1992; Harris and Freeman, 1993; Visscher et al. 1994). Differences are due to trait definitions, economic circumstances, and performance averages. The relative economic value of survival depends largely on the net cost of replacement (= cost of heifer minus salvage value cow) per year of herd life, which accounts for approximately 60% of the total (Dekkers, 1990; Allaire and Gibson, 1992; Visscher et al., 1994). The relative economic value is little affected by feed or milk prices, or by level of production

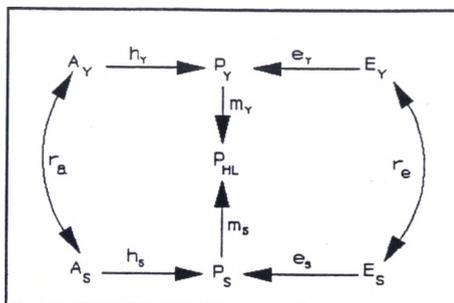


Figure 1. Model for HL, in which P, A, and E are phenotype, genotype, and environment, and h, e, r, and m are $\sqrt{\text{heritability}}$, $\sqrt{1-h^2}$, correlations, and partial regressions.

(Rogers et al., 1988; Visscher et al., 1994). However, Allaire and Gibson (1992) found the relative economic value to increase with level of production when a constant genetic variance was assumed for production instead of a constant coefficient of variation. They also found the relative economic value to increase with annual fixed costs per cow.

In the above, survival ability was defined on a lifetime basis. Kolstad and Dekkers (1994, unpublished) estimated economic values by lactation, using the model of Van Arendonk and Dijkhuizen (1985). Economic values, expressed per % reduction in involuntary culling within a lactation, decreased with parity from \$3 per cow per year in lactation 1 to \$.70 in lactation 6. Survival in the first three lactations accounted for over 65% of the economic value of lifetime survival. Changes with parity are mainly due to reductions in the number of cows present. Visscher et al. (1994) obtained similar results.

Conformation For producers who obtain limited income from sale of breeding stock, conformation traits have no direct economic value and should not be included in the breeding goal. Prices of breeding stock are, however, frequently influenced directly by conformation, in addition to the potential impact of conformation on herd life. Therefore, producers that sell breeding stock could consider including conformation in the breeding goal, provided this economic benefit persists into the future.

DEFINITION AND RECORDING OF TRAITS

Herd Life Many alternative definitions of traits related to HL have been suggested and investigated in the literature. They can be grouped into 3 main categories: (1) traits related to length of total or productive life (e.g., age at last calving or disposal; time from first calving to last calving or disposal (productive life); number of lactations or calvings); (2) survival up to a certain age, lactation, or length of productive life (stayability); and (3) survival within each consecutive lactation (Madgwick and Goddard, 1989). In addition to these categories, Ducrocq et al. (1988) distinguished between true (THL) and functional herd life (FHL). THL was defined as actual length of productive life, and FHL as the ability of the cow to survive regardless of production. FHL is obtained by a statistical adjustment of THL for production to get a measure that is more closely related to survival ability. The distinction between THL and FHL can be applied all 3 categories. Data on survival ability cannot be obtained directly.

Data on HL can be derived from data obtained through milk recording programs (birth and calving dates, and date and primary reasons for culling). Although Westell et al. (1982) found that reasons for culling contain little genetic information, their main use with regard to HL is to identify cows that are sold to another herd or exported. Data on FHL can be derived through adjustment of HL for production. In terms of the model: $P_{FHL} = P_{HL} - r_{Y,HL} P_Y = m_s(P_s - r_p P_Y)$, where $r_{Y,HL}$ and r_p are phenotypic correlations of production with HL and survival ability. Because the objective is to remove the effect of culling for production, the measure of production used in this adjustment should reflect the criterion producers use to incorporate producing ability into the culling decision. Therefore, a cow's phenotypic production deviation (Dekkers et al., 1994) or percentile ranking within the herd (Ducrocq et al., 1988) should be used rather than absolute production. Production in first, last, or averaged over lactations have been used for adjustment. Production in last lactation may, however, not reflect true performance ability of the cow, because it can be affected adversely by disease (Burke and Funk, 1993).

Conformation Most dairy populations have extensive classification programs for conformation traits, often organized by purebred associations. First and sometimes later lactation cows are scored by trained classifiers. In general, the aim of traits that are scored is to describe characteristics of the cow that are deemed important with regard to functionality and the breed. The number of traits, type of traits, and method of scoring differ from country to country. International efforts are currently underway to score a minimum of 12 standard traits (stature, body depth, rump angle and width, rear leg set, foot, fore udder, rear udder height, central ligament, udder depth, and teat placement and length) (World Holstein Friesian Federation, Classifiers Workshop, 1992). In many countries additional traits are recorded, including composite traits and an overall classification. Generally, traits are scored

subjectively on a linear descriptive scale (e.g., Thompson et al, 1983). However, scales and particular characteristics of traits differ from program to program. Further international harmonization of scoring methods is needed to allow accurate comparison of conformation traits across countries. Ideally, objective measurements should be used (Shannon et al., 1993).

GENETIC PARAMETERS

Herd Life, Survival Ability, and Production Heritability of HL depends on the trait definition. Visscher et al. (1994) showed that heritability of completed HL (category 1) can be 3 to 5 times higher than heritability of stayability or lactational survival (categories 2 and 3). The difference between heritability of FHL and THL depends on the amount of voluntary culling (Dekkers, 1993).

Most estimates of heritability of THL traits from category 1 range from .03 to .10 (e.g., Strandberg, 1985; Ducrocq et al., 1988; Boldman et al., 1992; Van Raden and Klaaskate, 1993). Estimates of heritability of THL traits in categories 2 and 3 are generally less than .05, with many below .03 (e.g., Strandberg, 1985; Van Doormaal et al., 1985; Dentine et al., 1987; Brotherstone and Hill, 1991; Visscher et al., 1994). Corresponding estimates for FHL traits are generally similar or slightly lower (e.g., Ducrocq et al., 1988; Boldman et al., 1992; Short and Lawlor, 1992; Jairath and Dekkers, 1994). Estimates of genetic correlations between stayability up to consecutive ages are generally high (>.8), both for THL (Strandberg, 1985; Dentine et al., 1987; Short and Lawlor, 1992; Van Doormaal et al., 1985) and FHL (e.g., Rogers et al., 1990). Part-whole relationships contribute to these correlations, as well as the common effect of production for THL traits. Visscher et al. (1994) also found high genetic correlations between survival within consecutive lactations (category 3), which may be due to the common effect of production. Jairath and Dekkers (1994) found lower (.6 to .75) genetic correlations between functional survival within each of the first three lactations. Several studies also indicate that HL is not the same genetic trait in different (sub)populations, in particular in registered versus grade herds (e.g., Dentine et al., 1987). These results are likely caused by differences in culling criteria.

Estimates of genetic correlations between THL traits and production traits have generally been positive, ranging from .3 to .9 (Strandberg, 1985; Short and Lawlor, 1992; Van Raden and Klaaskate, 1994; Visscher et al., 1994). Estimates of genetic correlations between FHL traits and production have been close to zero (e.g., Ducrocq et al, 1988; Short and Lawlor, 1992).

For development of effective selection programs, estimates of genetic parameters related to survival ability (involuntary culling) are needed (h_s^2 and r_a in Figure 1). However, survival ability can only be observed through its expression in HL, which is also determined by production (Figure 1). Several simulation studies (Essl, 1989; Strandberg, 1991; Dekkers, 1993) have shown that genetic correlations obtained from analysis of THL and production severely overestimate the genetic correlation between survival ability and production (r_a). Estimates can be up to +0.6 for negative true r_a , depending on the amount of voluntary culling. Biases depend on true parameters, which are unknown. However, a negative r_a is indicated by negative genetic correlations of production with health and fertility traits (e.g., Rogers, 1994). Genetic correlations between FHL and production are also biased estimates of r_a , because adjustment for production removes not only the direct effect of production on HL (m_v) but also the indirect effect (r_p) (Dekkers, 1993). Biases in estimates of r_a based on FHL change from negative to positive with increasing m_v , but are likely small for the amount of voluntary culling found in field data (Dekkers, 1993). Heritabilities of THL and FHL are also biased estimates of heritability of survival ability, however, biases tend to be smaller (Essl, 1989; Dekkers, 1993). These theoretical results indicate that estimates of genetic parameters of THL and FHL should be interpreted with care.

Conformation and herd life Heritability estimates of conformation traits are generally high (.25 to .45) for body traits (stature, size, angularity, body depth and strength, rump angle and width), moderate (.2 to .3) for udder conformation, and lower (.15 to .25) for feet and leg traits (Jamrozik et al., 1991; Short and Lawlor, 1992; World Holstein Federation, Classifier Workshop, 1992). Heritabilities depend on clear and objective recording of traits; measured traits have higher heritabilities (Shannon et al., 1993).

Estimates of genetic correlations between conformation and HL have not been consistent, but differ by breed, (sub)population (registered versus grade), and classification program (e.g., Dentine et al., 1987; Boldman et al., 1992; Brotherstone et al., 1991; Rogers et al., 1990; Short and Lawlor, 1992; Harris et al., 1992; Dekkers et al., 1994;). However, some general trends can be detected: genetic correlations between body traits and HL tend to be small positive ($<.2$) in registered herds, but close to zero or negative ($>-.2$) in grade herds. Correlations of udder conformation traits with HL tend to be moderately positive (.15 to .5), with highest correlations for udder depth and fore udder attachment. Correlations are higher for registered than grade cattle. Correlations between feet and leg traits and HL are variable, despite their perceived importance. This may be due to differences in trait definitions. Correlations of rear legs side view with HL are generally small ($<.1$), because this trait is scored on a scale with an intermediate optimum. When transformed to a scale that expresses desirability, Dekkers et al. (1994) found a significant positive genetic correlation with FHL (.2). However, the genetic nature of this trait is unclear. Genetic correlations of HL with overall type are generally moderate (.3 to .55) for registered herds, but smaller ($<.15$) for grade herds. Correlations of conformation traits with FHL tend to differ from those with THL only for traits that are correlated to production, as expected. For example, dairy character has a positive genetic correlation with THL, but tends to be uncorrelated with FHL. Stronger correlations between conformation and HL in registered versus grade herds are likely due to differences in culling criteria. Reported estimates should be interpreted in this light. In addition, correlations with HL may be biased estimates of correlations with survival ability (see previously).

GENETIC EVALUATION

Herd Life For selection purposes, genetic merit of animals must be evaluated based on information that is available early in an animal's lifetime. Therefore, genetic evaluations for HL must be able to utilize incomplete HL information on cows that are still in the herd when (sire) selection decisions are made. Proposed methods for genetic evaluation of HL can be separated into 3 groups that correspond to the 3 categories for HL trait definitions. For traits in categories 2 and 3, the problem of incomplete HL information is circumvented through definition of the trait that is analysed, which results in completed observations at an early age (e.g. stayability up to 42 months of age or to 17 months of productive life, and survival within consecutive lactations, all recorded as 0/1). Although logistic regression (DeLorenzo and Everett, 1992) or threshold models are preferred for genetic evaluation of these binary traits, most studies have used linear models. Biases are expected to be small (Meijering and Gianola, 1985). Single trait models can be used for traits in category 2 (stayability). Traits in category 3 can be analysed with a single trait repeatability model (Madgwick and Goddard, 1989) if survival in each lactation is the same trait. Otherwise, multiple trait models are needed (Jairath and Dekkers, 1994).

For genetic evaluation of traits in category 1, incomplete HL information needs to be handled within the method of analysis. Smith and Quaas (1984) introduced failure time analysis models for genetic evaluation of HL. These methods were later modified by Ducrocq et al. (1988). In these models, incomplete HL records are treated as censored. Van Raden and Klaaskate (1993) proposed prediction of completed HL for cows that are still in the herd. Genetic evaluations are then computed with a linear model, with less weight on predicted versus completed HL records. In this approach, variables to project incomplete records should be chosen with care, because they may be reflected in the evaluations.

Methods proposed for genetic evaluation of HL differ in several aspects:

- i) **The extent to which all HL information is utilized.** Evaluations based on stayability (category 2) do not utilize HL information that becomes available after the period considered for stayability. Although this has little impact on information available on a sire's daughters at the time of sire selection, it does limit utilization of additional HL information that is available through a sire's pedigree. Pedigree information is relatively important for low heritable traits. Methods based on survival by lactation (category 3) or on continuous HL (category 1) make optimal use of all HL information.
- ii) **The ability to account for systematic environmental effects.** Complete accounting for systematic environmental effects is important for accurate genetic evaluation, especially for HL, because of the

large impact of often changing management decisions and culling strategies throughout a cow's lifetime. Methods for traits in category 3 and the failure time analysis methods for traits in category 1 (Ducrocq et al., 1988) allow for time dependent fixed effects (e.g., herd-year). Other methods are limited to inclusion of fixed effects that pertain to first calving or first lactation.

iii) **Assumptions on the genetic characteristics of HL.** Methods for traits in category 1 implicitly consider survival as the same trait throughout the animal's life time. Methods for traits in category 3 allow for evaluation of survival by lactation as separate traits in a multiple trait model. Methods for traits in category 2 make no explicit assumption on the genetic nature of HL, but evaluations for survival in later stages of life are possible only as correlated estimates.

All methods allow for genetic evaluation of FHL traits by preadjusting data for production, or by including production in the model through fixed effects. In most studies, production is included as a common effect for all herds (Ducrocq et al., 1988; Boldman et al., 1992; Short and Lawlor, 1992). However, the amount of voluntary culling varies by herd and year, because of the dynamic nature of health problems and management strategies, changes in herd size, quota allotments, and differences in culling strategies between herds. Ducrocq (1994) and Jairath and Dekkers (1994) included interactions of production with change in herd size and season in the model to account for some of these differences. Additional differences in voluntary culling between herd-years could be accommodated by fitting within-herd covariates for production as random regressors (Schaeffer and Dekkers, 1994).

Conformation National genetic evaluations for conformation traits are computed on a regular basis in most countries. Single or multiple trait animal or sire models are used, with adjustments for herd-year-season, classifier, and age and stage of lactation at classification (World Holstein Friesian Federation, Classifier Workshop, 1992). In some cases, data are adjusted for heterogeneous variance between classifiers or herd-year-seasons, although the latter does not have a large impact (Koots et al., 1993).

USE IN SELECTION

For maximum genetic improvement in efficiency or profit, genetic evaluations (EBV) for traits that are related to traits in the breeding goal (production and survival in the current context) should be incorporated into a total merit index based on accurate genetic and economic parameters. Several studies have shown that incorporating EBV for HL into selection programs for production, can improve selection response for total merit by 2 to 4% (Allaire and Gibson, 1992; Dekkers, 1993; Rekik and Allaire, 1993). However, with availability of EBV for several alternative traits related to survival (THL, FHL, and conformation), an additional question is which trait(s) should be included in the index. Kennedy et al. (1993) showed that a selection index in which one trait is adjusted for one or more of the other traits in the index is equivalent to an index that includes the unadjusted traits. This suggests that a selection index with production and FHL is equivalent to an index with production and THL. However, Dekkers (1993) showed that an index based on FHL is more efficient than an index based on THL with regard to improvement of a breeding goal of production and survival ability, because biases in estimates of genetic parameters are smaller for FHL (see previously). The extent of bias in parameters is unknown and cannot be accounted for when deriving the corresponding indexes. Differences in efficiency of indexes are, however, small when survival ability is of lower relative economic importance than production. An additional reason why an index with FHL is more effective is because genetic evaluations for THL do not account for the nature of the relationship between production and HL. This includes nonlinearity of the relationship, but especially the negative covariance between genotype and environment for HL, which is introduced by culling on relative production. If not removed through a proper within-herd adjustment for production, as in FHL, this covariance results in misranking of sires across generations or when sires are evaluated based on progeny groups in herds that differ in genetic merit for production.

Several studies have proposed use of EBV for conformation traits as indirect measures of HL in a total merit index, especially because of their early availability (first lactation). With the large number

of conformation traits evaluated, extensive equations can be developed to predict sire EBV for FHL or THL based on selection index theory (Boldman et al., 1992; Harris et al., 1992) or multiple regression of sire EBV for conformation on HL of their daughters (Brotherstone and Hill, 1991; Dekkers et al., 1994). Several studies have estimated that these prediction equations can account for up to 60% of genetic variation in FHL or THL, although the accuracy of prediction is in general lower for grade herds (Boldman et al., 1992; Harris et al., 1992; Dekkers et al., 1994). Based on this, Boldman et al. (1992) indicated that indirect sire EBV for HL based on conformation are more accurate than direct EBV based on HL records, when the number of daughters is limited and they are early in their productive life. However, recently Visscher (1994) showed that the stated accuracy of indirect EBV based on a large number of traits can severely overestimate the real accuracy due to errors in genetic parameters; parameters are assumed known without error when deriving the prediction equations and their accuracy. To avoid this, indirect EBV for HL should be computed based on only a limited number of traits with a known biological relationship with survival ability. Other alternatives include bending of parameter estimates (Hayes and Hill, 1981).

Several studies have found nonlinear genetic relationships between conformation traits and HL (e.g., Dekkers et al., 1994). Theory on selection for nonlinear profit functions indicates that nonlinear selection indexes do not result in higher genetic gain than linear indexes (Goddard, 1983). Similarly, selection on conformation traits should be based only on their linear relationships with survival, especially given the uncertainty of relationships at the extremes. Nonlinear relationships could be incorporated in mating strategies, but benefits are expected to be small (Allaire, 1993).

Although selection on direct and indirect EBV for HL have been discussed separately, ideally selection for survival should be on a combination of EBV for conformation traits and direct EBV based on HL records. When combined in a multiple trait setting, this would capitalize on the early availability of conformation traits relative to HL information.

GENERAL DISCUSSION

Herd life is a complex trait and is highly influenced by culling criteria of producers. Genetic evaluations for HL reflect producer decisions and perceptions, and may not be an objective indicator of functionality in all aspects. This is evidenced by the less than unit genetic correlation between HL in different (sub)populations and the stronger genetic relationships between conformation and HL in registered versus grade herds. Although these differences may be due to different economic circumstances (e.g., sale of livestock), they are partly the result of differences in breeder perceptions, especially with regard to conformation. It is unclear whether the stronger association between HL and conformation in registered herds is justified with regard to functionality. Research to determine the appropriate role of conformation in breeding programs should focus on associations with specific health disorders rather than on observed HL. EBV for HL may also be affected by popularity of the bull or by differential culling of daughters of, e.g., young versus proven bulls.

Genetic evaluations for HL and conformation can aid genetic improvement in dairy cattle if properly incorporated in selection strategies and reduce or reverse negative correlated responses in health and survival ability that are associated with intense selection for production. However, given the problems and potential biases associated with EBV for HL and their limitations as complete indicators of economic merit for traits other than production, EBV for HL should be considered as an intermediate step towards development of selection strategies based on genetic evaluations or indicators for fertility and resistance to disease (Rogers, 1994). Implementation of such genetic evaluation systems will require establishment of more detailed large scale recording systems for health and fertility traits than are currently available in most countries.

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