Feed Intake Specifications in Defining Breeding Objectives

D. R. Notter
Virginia Polytechnic Institute and State University

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FEED INTAKE SPECIFICATIONS IN DEFINING BREEDING OBJECTIVES

D. R. NOTTER, USA
Virginia Polytechnic Institute and State University
Blacksburg, VA 24061

SUMMARY

Development of selection objectives for beef cattle requires consideration of the available feed resources. In production systems with access to liberal quantities of harvested feeds of relatively high quality, selection to improve economic efficiency will normally favor animals with high genetic potentials for the primary production traits. However, these highly productive types may also have relatively high maintenance requirements and be less efficient when nutrient restrictions prevent expression of genetic differences in appetite. Thus, important genotype x environment interactions may be observed. In range environments, animals may be restricted in the amount of forage that can be harvested. These restrictions usually arise from an inability of the animal to increase grazing times or feed intake rates beyond certain levels imposed by the sward and by innate animal requirements for rest and rumination. In addition, maintenance requirements are often elevated in range environments, thereby further limiting the increases in productive capacity that can be accommodated. Under conditions of nutrient restriction, antagonistic phenotypic relationships may also be observed among production traits (such as milk production and reproduction). The nature of these relationships must be considered in the development of selection criteria.

INTRODUCTION

In all livestock species, development of selection goals and associated selection criteria must involve consideration of the food resource that is available for exploitation. For animals maintained in relatively benign environments and fed harvested feeds at levels designed to meet estimated nutrient requirements, selection for net economic merit usually promotes increases in absolute rates of production. Thus, in the North American dairy cow, the absolute rate of milk production has served as the primary factor associated with genetic improvement in profitability. Likewise, for swine raised in confinement, increases in number of pigs weaned per sow bred and in total or lean tissue growth rate (depending upon the marketing system) appear most important (Tess et al., 1983).

Development of optimum weightings for performance traits for use in selection requires knowledge of the interrelationships among dietary characteristics, feed intake and rate and composition of gain in market animals and between feed intake and reproductive performance in breeding animals. For confinement-reared species, these relationships can usually be obtained experimentally and coupled with estimates of genetic parameters and cost-price relationships to define overall economic efficiency. This result is partly a reflection of the control of feed inputs by the manager and partly a result of the more homogeneous production environment found in confinement.

Development of selection criteria for completely or partially free-ranging ruminants is more difficult because of the complex ecology of these
animals. Also, production objectives for free-ranging grazers differ from those of housed livestock. In confinement, profit is defined by the efficiency with which harvested feeds provided at controllable levels are utilized by a controllable number of animals to produce saleable products. In pastoral systems, profit is determined by the efficiency with which a controllable number of animals utilizes a feed resource that varies in quality and quantity within and among years and is harvested directly by the animal in a manner that is incompletely understood. The harvesting process may be biologically inefficient (i.e., percentage of available nutrients harvested or percentage of harvested nutrients recovered in animal products) but is often economically very efficient (cost per unit animal product).

The feed resources of grazing animals can be influenced profoundly by man, but their control is at best a two-step process involving both plant and animal responses, and, perhaps more importantly, usually involves a multispecies response at the plant (pasture) level. The management of grazing animals likewise often involves partition of a fixed land area to alternative plant production systems and also includes the option of providing more costly supplemental harvested feeds. Thus, the relationships necessary to understand pastoral production systems and the likely responses of the production system to genetic changes can be extremely complex.

RESULTS AND DISCUSSION

Effects of Feed Intake Specifications on Expression of Genetic Differences in Rate and Efficiency of Growth.

A considerable body of data suggests that if market cattle are fed harvested feeds of relatively high quality (>65% digestible dry matter) and slaughtered at a constant level of fatness, differences among genetic types in efficiency of gain are small (Smith et al., 1976; Cundiff et al., 1981; Southgate et al., 1982a,b). However, differences among breeds in efficiency of gain have been observed when less digestible diets were fed for a portion of the finishing period (Southgate et al., 1982b; Webster, 1985).

In particular, Webster (1985) has suggested that breed differences in appetite on high-energy diets may be positively related to differences in fasting metabolic rate. Such a relationship would allow proportionately higher rates of metabolizable energy (ME) intake by breeds with higher basal maintenance requirements (MEM; Mcal ME) and would, therefore, allow faster gains at no lower efficiency for these types. [I.e., if ME intake (MEI) is proportional to MEM such that MEI = αMEM, the ME available for production (MEP) will be MEP = (α - 1) MEM and efficiency of energy use will be MEP/MEI = (α - 1)/α which is independent of MEM.] However, on low-quality diets (< 65% digestible dry matter; Conrad et al., 1964), appetite tends to be regulated by rumen fill instead of by metabolic feedback mechanisms and the proposed relationship between appetite and MEM would no longer hold. In such a situation, an increase in MEM would be detrimental because compensating increases in MEI could not occur and efficiency would be lower for types with higher metabolic rates. [I.e., if MEI is constant, MEP = MEI - MEM and MEP/MEI = (MEI - MEM)/MEI and decreases as MEM increases.]

Ferrell and Jenkins (1985) reviewed the maintenance requirements of different cattle types and concluded that maintenance requirements appear to be positively associated with the genetic potential for production.
In general, maintenance requirements appear highest for dairy types and lowest for Bos indicus breeds and crosses. Ferrell and Jenkins further concluded that the higher rates of heat production in more productive types may be specifically associated with a higher protein synthetic capacity of the liver and gut.

Taylor et al. (1981) estimated the repeatability of weight maintained by twin Aryshire cattle at different intake levels at .70. The estimated genetic coefficient of variation for maintenance efficiency was 6.4%, a value similar to the genetic coefficient of variation for yearling weight reported by Brinks et al. (1964).

Thus improvement in rate and efficiency of gain should occur in response to direct selection, but correlated responses in basal heat production may differ among feeding environments. The heritability of growth rate may be lower in grazed cattle (Menissier et al., 1984), but substantial response to selection for growth has occurred under grazing conditions (Baker et al., 1980). In particular, Frisch (1981) reported that much of the response to selection for growth in a harsh, tropical environment was attributable to decreased maintenance requirements and improved adaptability.

Inconsistent relationships between MEM and growth in different environments have important implications for performance-testing programs. Dalton and Morris (1978) and Menissier et al. (1984) reviewed several aspects of central performance testing programs; both concluded that realized correlations between performance in the central test and subsequent progeny performance have been disappointingly low. Langholz et al. (1984) compared the performance of progeny of nine Friesian bulls under concentrate, silage or pasture feeding. Rank correlations involving measures of progeny growth in different environments were not significant and important sire rerankings occurred among environments.

A particular area of concern with regard to sire x environment interaction relates to the extent to which expected progeny differences (EPD's) among sires progeny tested in purebred herds will be expressed in the more restrictive nutritional environments that are common in commercial herds. Beginning in 1982, Polled Hereford sires were chosen based on EPD's for yearling weight and maternal weaning weight (APHA, 1985) and mated to Angus cows at the Shenandoah Valley Research Station in Virginia. Calves were not creep fed; 205-d weaning weights averaged 195 kg. Heifers were wintered on corn and corn silage at levels consistent with mating at 15 mo of age. Table 1 shows means and ranges for sire EPD's and corresponding regressions of progeny means on sire EPD's and dam most probable producing abilities for weaning weight (MPPA). The relationship between progeny birth weight and birth weight EPD did not differ from 1.0, but no significant relationship was observed between progeny weaning weights and sire EPD's for either weaning or yearling weight. A probable nutritional basis for this poor relationship is suggested by the subsequent strong relationship between 19-mo heifer weight and yearling weight EPD and by the very strong relationship between weaning weight and dam MPPA (2.29 ± .42 kg/% in ratio units, or approximately 1.17 kg/kg). Therefore, in this environment, genetic superiority of sires for weaning weight in purebred herds did not confer an advantage in progeny weaning weight. Milk production of the dam (as indicated by MPPA) was apparently much more important.

**Table 1.** Means, regression coefficients, and range of differences for progeny BW and MPPA.

<table>
<thead>
<tr>
<th>Type</th>
<th>BW, WW and 19-mo Weaning Ability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Progeny BW o</td>
<td></td>
</tr>
<tr>
<td>Progeny WW o</td>
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<tr>
<td>Progeny WW o</td>
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</tbody>
</table>

**Regressions**

- Range
- Basis

18 sires in *p < .05

Ochoa et al. increased from 0 to 29.00 kg of transmission upon the nutritive activity.

Grazing process involving providing plus or shelter within broad climate. However, ever climate, grazing success and apparently much more important.
TABLE 1. MEANS AND RANGES FOR SIRE EXPECTED PROGENY DIFFERENCES (EPD) FOR BIRTH (BW), WEANING (WW) AND YEARLING (YW) WEIGHTS AND REGRESSIONS OF PROGENY BIRTH, WW AND 19-MO HEIFER WEIGHTS (HW) ON SIRE EPD'S AND DAM MOST PROBABLE PRODUCING ABILITIES (MPPA)

<table>
<thead>
<tr>
<th>Sire mean EPD (kg) for: a</th>
<th>Progeny mean (kg) for: b</th>
</tr>
</thead>
<tbody>
<tr>
<td>BW</td>
<td>WW</td>
</tr>
<tr>
<td>+ .9</td>
<td>+9.0</td>
</tr>
<tr>
<td>(-.5 to +4.8)</td>
<td>(-2.1 to +22.2)</td>
</tr>
</tbody>
</table>

Regressions of:

Progeny BW on EPD-BW = .72 ± .31 kg/kg*
Progeny WW on EPD-WW = .15± .26 kg/kg
Progeny YW on EPD-YW = .13 ± .16 kg/kg
Progeny HW on EPD-YW = .96 ± .48 kg/kg*
Progeny WW on MPPA = 2.29 ± .42 kg/kg**

aRange in EPD’s is given in parentheses.
bBased on 271 progeny by 43 sires over 3 yr for BW and WW; 56 progeny by 18 sires in 1 yr for HW.
*p < .05; ***p < .001.

Ochoa et al. (1981) reported that the repeatability of weaning weight increased from .30 to .52 and the variance in cow MPPA increased from 6.22 to 29.00 kg² when calves were not creep fed. Thus, the relative importance of transmitted and maternal effects on weaning weight may depend importantly upon the nutritional environment.

Effects of Grazing Behavior on Expression of Genetic Differences in Productivity.

Grazing animals must harvest the nutrients that they require. This process involves alternating periods of grazing, rumination, resting and idling plus time spent moving to and from water and, if necessary, shade or shelter. Time spent grazing and the rate of grazing can be adjusted within broad limits to allow the animal to meet its nutrient requirements. However, even under conditions of liberal forage availability and mild climate, grazing times seldom drop below 7 to 8 h (Stobbs, 1974; Chacon et al., 1978; Jamieson and Hodgson, 1979a).

As the productive capacity of a herd increases, the animals must harvest progressively more feed. This increase can be achieved by increasing the rate and/or time of grazing. Alden and Whittaker (1970) defined the herbage intake of the grazing animal as the product of grazing time (h), biting rate (bites/h) and bite size (g/bite). Thus, an increase in intake requires an increase in one or more of these components.

Much of the research on grazing behavior of cattle pertains to tropical pastures (Stobbs, 1973a,b, 1974, 1975) but similar work on temperate pastures also exists (Jamieson and Hodgson, 1979a,b; Zoby and Holmes, 1984). These results, taken together, suggest certain limits on the ability of grazing animals to ingest forages from pasture. Normal grazing times rarely exceed 10 to 12 h for cattle (Stobbs, 1975), although grazing times in excess of 12 h have been recorded (Arnold and Dudzinski, 1978). Likewise, biting rates rarely exceed one bite/sec in either cattle or sheep (Alden and Whittaker, 1970; Chacon and Stobbs, 1976; Arnold and Dudzinski, 1978), and Stobbs (1975)
reported that cattle seldom take more than 36,000 grazing bites per day. Bite sizes for mature, nonlactating Jersey cows grazing tropical pastures have ranged from .066 to .34 g organic matter (OM)/bite (Stobbs, 1974; Chacon and Stobbs, 1976). Similar cows had mean bite sizes of .43 g OM/bite on immature temperate pastures (Stobbs, 1974) and of .39 to .80 g OM/bite when fed harvested tropical forages (Stobbs, 1973a, 1974). On temperate pastures, bite sizes for Friesian calves of 121 to 175 kg ranged from .110 to .365 g OM (Jamieson and Hodgson, 1979a,b). Constraints on grazing time may relate to fatigue (Stobbs, 1975) or to requirements for rumination. Cattle usually ruminate for 5 to 9 h/d (Arnold and Dudzinski, 1978). The ratio of rumination time to grazing time tends to be proportional to cell wall intake (VanSoest, 1983) and can range from .85 to .95 for large ruminants consuming low-quality forages (Lofgreen et al., 1957; Sinclair, 1977). Sinclair (1977) reported that total feeding activity (grazing plus ruminating) by African buffalo during the dry season encompassed up to 19 h/d.

At least four situations can be envisioned in which feed intake by grazing cattle can be held to levels that are inconsistent with genetic increases in productivity. First, in tropical pastures, the distribution of leaves throughout the plant canopy may be such that harvesting of leaves without excessive ingestion of stem and inflorescence may strongly limit bite size. This is the situation addressed by Stobbs (1973a,b, 1974) and pertains primarily to tropical pastures (see Hetzel, 1986).

Second, in more uniform temperate swards, reductions in tiller length associated with heavy grazing may limit intake. Allden and Whittaker (1970) reported that daily intakes by sheep grazing ryegrass could be maintained at constant levels at tiller lengths between 8 and 35 cm but dropped precipitously at tiller lengths below 8 cm. Importantly, Allden and Whittaker also reported that 43-kg wethers consumed forage dry matter (DM) much more rapidly than did 25-kg lambs at tiller lengths of 40 cm (8 vs 5 g DM/min), but at tiller lengths of 7 cm lambs had higher eating rates than did the wethers (1.8 vs .9 g DM/min). Thus, smaller animals were more capable of harvesting short forage than were larger animals. Zoby and Holmes (1984) reported that at low stocking rates (745 kg herbage/animal), bite sizes were proportional to the .75 power of weight in cattle between 163 and 624 kg, and daily OM intake was proportional to the .45 power of weight. At high stocking rates (178 kg herbage/animal), bite size and OM intake were proportional to the .52 and .26 powers of body weight, respectively. On closely-managed pastures, problems in availability due to tiller length can be avoided by controlled access and rotational grazing. However, in extensive grazing areas or in situations in which inconsistent rainfall patterns may force periodic overgrazing, animals may be restricted to short forages for considerable periods.

Thirdly, the distribution of high-quality plant material throughout the pasture may, in some situations, foster a "search and destroy" grazing strategy in which alternating periods of walking (searching) and short periods of grazing occur. These situations seem most likely in heterogeneous environments with non-uniform topography. An increase in intake in such environments requires either an increase in foraging effort (time spent, distance covered and/or speed of foraging) or a reduction in selectivity and, therefore, in diet quality. Demment and VanSoest (1983) document that small ruminant species graze more selectively than do large ruminant species. This result reflects the relatively higher maintenance requirements of smaller species.
in relation to their gut capacity as well as the fact that the most abundant forage parts in most environments are those with higher cell wall contents. Thus, ingestion of large volumes of food tends to preclude selectivity. For a larger or more productive animal to maintain a sufficient intake of a sparsely-distributed forage without a reduction in diet quality, the animal must graze over a larger area. Reliable estimates of the relationship between body size and foraging area are not available. However, on theoretical grounds (Alexander, 1977), the distance that can be traversed in a constant time by animals of different sizes walking at "comparable" speeds tends to vary with the square root of leg length and leg length tends to vary with the 1/4 to 1/3 power of body weight. Thus, the distance walked per unit time probably at best increases with the .12 to .17 power of body weight, suggesting that if the preferred forage is rare, an increase in foraging radius is unlikely to compensate for the increases in nutrient requirements associated with increased size.

Lastly, climatic stress may limit the animal's ability or willingness to forage. In hot, humid climates (Hetzel, 1986), inability to dissipate heat may limit grazing time and promote idling in shaded areas. Heat stress alone appears unlikely to prevent animals from meeting their basic requirements for maintenance and lactation in suckler herds but may reduce the marginal feed intake required to support more "optional" productive functions such as growth with fattening or milk production in dairy herds. In cold environments, additional energy may be required to maintain thermal equilibrium, although the magnitude of this increase can be reduced by physiological adaptation to cold (Young, 1983). However, under extreme cold stress (including wind and moisture), cattle may reduce grazing time in order to save heat through postural adjustments (lying) and sheltering, and "optional" production functions may again suffer.

Figure 1 presents estimated ME requirements for 450 or 650 kg cows grazing under favorable or more restrictive conditions. Values were derived from ARC (1980) assuming a metabolizability of the diet of .5; basal maintenance requirements (MEM) of .112 Mcal/kg·75; an activity requirement (MEA) of [.0004 + .000000478 d(1 + 14s)] Mcal/kg where d = distance walked (m) and s = average slope; and a requirement for maintaining body temperature (MEC) of [(.2843 -.006527)W-.66 - MEM - MEA] for temperatures below about 10 C and where W is weight. Favorable conditions assume a mean temperature of 0 C and walking 2.5 km/d at a 3% slope. Restrictive conditions assume a mean temperature of -10 C, an increase of 50% in the intercept of the activity equation (to .0006) and walking of 8 km/d at a 6% slope.

These results suggest that total maintenance costs at pasture may be 40 to 80% higher than MEM, a figure consistent with those reported by Arnold and Dudzinski (1978). The value of (MEM + MEC) increased with approximately the .5 power of weight, supporting the contention that larger types are better adapted to cold environments (Searcy, 1980). However, (MEM + MEA) increased with about the .8 power of weight. For (MEM + MEA) in the harsh environment and with an additional requirement of .04 Mcal ME/kg·75 body weight for milk production, a 450 kg type would require 18.29 Mcal ME or 8.66 kg/d of 60% digestible OM. A 650 kg type would require 24.53 Mcal ME or 11.62 kg/d of OM. At 36,000 bites/d, mean bite sizes of .24 g for 450 kg types and .32 g for 650 kg types would be required, suggesting possible intake limitations under certain grazing conditions for the larger types.
Figure 1. Metabolizable energy (ME) requirements for basal metabolism (MEM), activity (MEA) and cold (MEC) and total ME requirements for 450 or 650 kg cows in relatively mild (hatched bars) or relatively harsh (open bars) environments.

Effects of Feed Intake Specifications on Genetic Differences in Overall Economic Efficiency.

The nutritional environment can influence relationships among the various performance traits that jointly define the net economic efficiency of the production system. If intake is restricted, genetic mechanisms that act to limit the impact of that restriction on the overall ability of the animal to function will usually be favored. Thus, genetic types are required that can maintain acceptable levels of all primary productive functions (growth, gestation, lactation, reproduction) in the environment of interest. In particular, if a clear priority of nutrient use exists between competing productive functions, animals with high genetic potentials for some traits may be unable to maintain acceptable performance levels for competing traits. For example, high basal metabolic rates can limit the supply of energy available for growth and lactation. Likewise, cattle with high milk production potential may be unable to maintain sufficient condition to allow satisfactory calf survival (at very low milk levels) or fertility (at high milk levels). The feasible range was quite broad in good environments but was sharply constricted in poorer environments.

Holloway et al. (1975a,b) have shown that genetic increases in milk production potential can sharply limit reproduction and overall efficiency of production if the plane of nutrition is not increased to accommodate the animals' greater productivity. Results of computer simulation (Notter et al., 1979) suggest that for a given environment, a feasible range of milk production levels can be defined. Milk levels within the feasible range are potentially optimal, depending upon the relative costs of forage and concentrate feeds. Production levels outside the feasible range, however, are incompatible with acceptable calf survival (at very low milk levels) or cow fertility (at high milk levels). The feasible range was quite broad in good environments but was sharply constricted in poorer environments.

In developing selection criteria, one must be aware of potential antagonisms among production traits such that improvement in genetic merit for one trait may limit expression of the genetic potential for other traits. These antagonisms act at a phenotypic rather than genetic level as shown in the path diagram in figure 2A.
Path coefficient diagrams showing antagonistic phenotypic relationships between milk production and reproduction. Symbols are defined in the text.

In the diagram, calf weaning weight per cow exposed (WW) is taken as the selection objective and is presumed to be defined by the dam's reproduction (R, %) and milk production (M; expressed as kg calf weight) such that $WW = 1.88R + 0.82M$ (from Hepp, 1982). [Other factors influencing WW will be ignored for simplicity and included as error ($E_{WW}$). Distributional problems in measuring reproductive traits will also be temporarily ignored.]

Genetic (G) and environmental (E) correlations between R and M of .2 are assumed. Genetic and environmental variances of 160 and 1440 $\sigma^2$ for R and of 349 and 814 kg$^2$ for M are assumed and correspond to heritabilities of .3 for M and .1 for R in an unrestricted environment. The aggregate genotype (H) is given by $H = 1.88G_R + 0.82G_M$. Figure 2A also includes provision for a direct phenotypic effect of milk production on subsequent reproduction (the path M → R = d). Thus, the diagram assumes that genetic potentials for M and R may be positively correlated but that expression of genetic superiority in R can be masked by phenotypic effects of M. This assumption is supported by the favorable reproductive performance of dairy breeds at young ages but not at older ages (when cumulative effects of lactation may become more important; Willham, 1974).

In an unrestricted environment (d = 0), path coefficients (figure 2A) are:

$$
\begin{align*}
  a_1 &= .295 \\
  a_2 &= .794 \\
  a_3 &= .438 \\
  b_M &= .548 \\
  b_R &= .316 \\
  e_M &= .837 \\
  e_R &= .949 \\
  h_M &= .548 \\
  h_R &= .316 \\
  v_1 &= .498 \\
  v_2 &= .774 \\
  r_G &= r_E = .20
\end{align*}
$$
The phenotypic correlation of M with R (rp) is .193 and the optimum selection index is I = .285 M + .165 R.

If a negative relationship exists between M and R such that the regression of R on M = -.385%/kg (from Notter et al., 1979, for high milk levels), path coefficients in figure 2A become:

\[
\begin{align*}
    a_1 &= .323 \\
    a_2 &= .861 \\
    a_3 &= .480 \\
    d &= -.331 \\
    e_R &= .958 \\
    h_R &= .319 \\
    h_M &= e_M = r_G = r_E = \text{do not change}
\end{align*}
\]

(2)

h_M, e_M, r_G and r_E do not change but rp is reduced to -.136. The diagram is redrawn in figure 2B to specifically show negative effects of G_M and E_M on R. In that figure for this example, i_E = -.277 and i_G = -.181. H must be redefined so that v_1 is the total direct effect of G_M on H including direct effects of G_M on both M and R. Thus H = 1.88 G_R + .095 G_M and differs from the phenotypic regression of WW on R and M. In effect, the equation for H recognizes that increases in G_M will lead to negative effects on R and assigns G_M correspondingly less weight. The optimum index is now I = .134 M + .179 R and places much less emphasis on M.

An alternative approach would be to replace the r_G and r_E of .2 obtained in the unrestricted environment with realized correlations obtained in the environment of interest and to ignore direct effects of M on R (i.e., assume d = 0). However, this approach is not strictly appropriate because it assumes a bidirectional rather than unidirectional negative relationship between M and R. If H = 1.88 R + .82 M (i.e., use the same coefficients as the phenotypic regression) and if realized genetic parameters are calculated from the phenotypic regression of offspring on dam in figure 2B, the realized model becomes that shown in figure 2A with coefficients:

\[
\begin{align*}
    a_1 &= .323 \\
    a_2 &= .861 \\
    a_3 &= .480 \\
    d &= 0 \\
    r_G &= -.352 \\
    r_E &= -.091 \\
    r_P &= -.136 \\
    v_1 &= .632 \\
    v_2 &= 1.029 \\
    h_M &= e_M = r_G = r_E = \text{do not change}
\end{align*}
\]

(3)

The optimum index is I = .197 M + .224 R and assigns slightly less weight to R than does the index derived from figure 2B. If true H = 1.88 R + .095 M (as shown in figure 2B), the index derived from (3) would produce a selection response that is essentially equivalent to that of the best index. However, it may be easier to obtain the necessary phenotypic relationship, d, than to estimate r_G separately for each environment. In contrast, the index derived for the unrestricted environment (d = 0) would produce 12.5% less response than the best index derived for d < 0 (figure 2B).

These results suggest that the nutritional level may have important implications for the development of selection criteria, especially in the presence of nutritionally-mediated phenotypic antagonisms among traits. The effects of these antagonisms can be accounted for by quantification of the phenotypic relationship or by adjustment of realized genetic correlations and should be considered in defining the aggregate genotype.
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