The influence of dietary energy concentration and feed intake level on feedlot steers 1. Digestibility of diets and rumen parameters

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Received 22 February 1991; revised 3 September 1991; accepted 13 January 1992

Three ruminally cannulated mature steers were fed, in a crossover design, diets with concentrate to roughage (C:R) ratios of 80:20, 55:45 and 30:70, twice a day (09:00 and 15:30) in a predetermined feed intake sequence of *ad libitum*, 80% *ad libitum* and 90% *ad libitum*. Following the faeces collection period of 12 days, ruminal contents were removed at 2 h post feeding and were weighed, mixed, sampled and returned. DM intake decreased and then increased (non-linear; $P \leq 0.01$) as C:R ratio increased. DM digestibilities of the three intake levels were respectively 72.9, 73.8 and 76.1% for the 80:20 diet, 64.9, 65.0 and 65.1% for the 55:45 diet and 55.3, 56.3 and 57.1% for the 30:70 diet. DM digestibility was not influenced ($P = 0.28$) by feeding level, but was linearly reduced ($P \leq 0.05$) as C:R ratio decreased, which indicated that no significant associative effect had occurred. Both a decrease in feeding level and in C:R ratio increased rumen OM retention linearly ($P \leq 0.01$). Volatile fatty acid concentration (VFA) 2 h post-feeding was not influenced ($P \leq 0.05$) by feeding level, but was reduced linearly ($P \leq 0.01$) by a decrease in C:R ratio. A decrease in C:R ratio increased the molar percentage acetic acid and decreased propionic acid linearly, while feeding level had no significant influence. The lowest rumen pH (6.1) 2 h post feeding occurred at 80% of *ad libitum* on the 80:20 diet, which indicates that the ruminal environment was relatively stable on all treatments.

Drie rumen-gekannuleerde volwasse osse het in 'n omslagontwerp diëte met kragvoer-tot-ruvoer(K:R)-verhoudings van 80:20, 55:45 en 30:70 twee keer per dag (09:00 en 15:30) in die vooraf-vasgestelde volgorde van *ad libitum*, 80% *ad libitum* en 90% *ad libitum* ontvang. DM-inname het aansienlik verlaag en daarna toegeneem (nie-lineêr; $P \leq 0.01$) met 'n toename in die K:R-verhouding. Direk na die faecesversamelingperiode van 12 dae is die rumen-inhoud 2 h na voeding verwyder, geweeg, gemeng, bemonster en teruggeplaas. DM-verteerbaarhede vir die drie voedingspeile was onderskeidelik 72.9, 73.8 en 76.1 vir die 80:20-dieet, 64.9, 65.0 en 65.1 vir die 55:45-dieet en 55.3, 56.3 en 57.1% vir die 30:70-dieet gewees. DM-verteerbaarhede is nie deur die voedingspeil ($P = 0.28$) beïnvloed nie, maar het lineêr ($P \leq 0.05$) verlaag met 'n daling in die K:R-verhouding wat aandui dat betekenisvolle assosiatiewe effekte afwesig was. 'n Daling in beide die K:R-verhouding en voedingspeil het OM-retensietyd lineêr ($P \leq 0.01$) verlaag. 'n Daling in die K:R-verhouding verlaag die vlugtige-vetsuur(VVS)-konsentrasie en molare persentasie propionsuur lineêr, terwyl die molare persentasie asynsuur lineêr verhoog het. Voedingspeil daarenteen het geen betekenisvolle invloed op dié parameters gehad nie. Die laagste rumen-pH (6.1) 2 h na voeding het by 80% van *ad libitum* op die 80:20-dieet voorgekom en dui aan dat 'n relatief stabiele rumenomgewing by al die dieet-behandelings voorgekom het.

Keywords: Dietary energy concentration, digestibility, feeding level, steers.

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Introduction

The primary objective of the beef industry is the efficient production of high quality lean carcasses. Different nutritional strategies may be applied to produce such carcasses economically in South Africa. The choice of such strategies depends among other factors on the relative importance of maximum vs. optimum growth and feed efficiency. Owing to a paucity of data in this field, this study was conducted to investigate the influence of different dietary energy concentrations and feed intake levels on digestibility, feed intake, growth, feed efficiency and carcass composition.

Energy intake is the main factor affecting growth in beef cattle (Andersen, 1978). Increasing energy intake correspondingly increases daily gain. In the semi-intensive and intensive beef industries, energy intake is manipulated primarily by using divergent concentrate to roughage (C:R) ratios for the growing and finishing of cattle at various growth rates. However, negative interactions or associative effects between roughages and concentrates may occur, which reduce the amount of energy available for production. These associative effects depend, among other factors, on the type, amount and physical form of the roughage and grain source, all of which influence the pattern of fermentation in the rumen (Mould, 1988). Beef cattle fattened for slaughter usually are given *ad libitum* access to feed to maximize rate of gain and, presumably, feed efficiency, because maintenance cost is diluted. However, recent studies summarized by Hicks *et al.* (1987) challenged this assumption. Restricting intake by an average of 8.7% below *ad libitum* reduced daily gain by 5.2%, but improved feed efficiency by an average of 3.2%. An increase in diet digestibility due to reduced rate of passage (Peter, 1987) is among the several reasons proposed for this improvement.

The purpose of this study was to quantify the effect of an increase in the C:R ratio and feeding level on DM digestibility of maize hominy chop based diets by steers. Treatment effects on volatile fatty acid concentration, molar percentages of VFA, rumen pH and rumen OM retention time also were studied. These parameters may help detect whether differences in energy intake between treatments are due to associatives effects, rumen instability or digesta passage rate.

Materials and Methods

Animals and diets

Three ruminally cannulated mature Bonsmara steers were fed, in a crossover design, three diets with a C:R ratio of 80:20, 55:45 and 30:70 in a predetermined sequence of *ad libitum* (AL), 80% *ad libitum* (80AL) and 90% *ad libitum* (90AL). Daily feed allowance for the AL groups was about 10% more than *ad libitum*, based on air-dry feed intake of the previous three days. Diets were formulated to be isonitrogenous; formulations together with chemical analyses are shown in Table 1. Diets were mixed by a commercial manufacturer and delivered on a regular basis. The 90AL and 80AL feeding levels were calculated from mean air-dry feed intakes of the individual steers achieved in the AL feeding period. Steers, housed in individual pens, had access to water at all times and were fed two equal portions at 09:00 and 15:30 daily. Steers were adapted to their diets for 14 days before commencing with the first *ad libitum* experimental period. The 27 experimental periods lasted 12 days each with diet adaptation periods between feeding levels of 3 to 6 days and between diets, depending on diet sequence, of 4 to 16 days.

Table 1 Ingredient and nutrient composition of experimental diets

Item	Concentrate : roughage		
	80:20	55:45	30:70
Ingredients (g/kg, air-dry basis)			
Eragrostis tef hay[a]	200	450	700
Hominy chop	683.5	401.5	110.5
Molasses	50	50	50
Sunflower oil cake	28	65	112
Urea	11	8	5
Salt	4	4	4
Calcium phosphate	7.5	7.5	7.5
Limestone	10	9	7
Sodium bicarbonate	5	4	3
Vitamin and mineral premix[b]	1	1	1
Lasalocid[c] (mg/kg)	30	30	30
Tylosin[c] (mg/kg)	10	10	10
Nutrients (g/kg, dry-matter basis)[d]			
Crude protein (N × 6.25)	136	126	129
Crude fibre	147	239	315
Calcium	8.6	7.9	8.7
Phosphorus	4.4	4.4	3.8
Ether extract	46.0	21.0	19.6
Metabolizable energy (MJ/kg)[e]	12.0	10.6	9.2
Crude protein : metabolizable energy	11.3	11.9	14.1

[a] Hammermilled, 25-mm screen.
[b] Commercial premix.
[c] Active ingredient.
[d] Chemical analysis.
[e] Based on tabular values of feedstuffs.

Measurements and analyses

During the 12-day collection period, total faeces of individual steers, collected daily at regular intervals from the floor, was weighed, mixed, and sampled and its DM was determined. Dry-matter intake was determined daily. Upon completion of faeces collection periods, the contents in the reticulorumens of the steers were quantitatively removed at 11:00, 2 h after the morning feeding, and were then weighed and mixed. Samples of digesta were taken immediately for the determination of DM, organic matter (OM), starch content (MacRae & Armstrong, 1968), pH and volatile fatty acids (VFA), and the digesta were returned to the rumen. Ruminal fluid was preserved by adding 1 ml of a 10% NaOH solution to 9 ml rumen fluid. Dried faecal samples composed for each animal, and samples of the different diets milled through a 1-mm screen, were subsampled for chemical analyses.

The DM content of diets and faeces was determined by drying at 100°C for 24 h. Composite samples of the different diets were analysed for crude fibre, ether extract, calcium, phosphorus and crude protein (N × 6.25) according to the methods of the Association of Official Analytical Chemists (AOAC) (1984). VFAs were determined by gas chromatography (Suzuki & Lund, 1980).

OM retention time (h) was calculated as the ratio of OM contents in the reticulorumen (kg) × 24h and the mean OM intake (kg). Owing to differences in feeding pattern between different feeding levels it was expected that the reticulorumen OM content, based on a single evacuation 2h post fed, probably would not result in comparable OM retention times between feeding levels. However, OM retention times between C:R ratios should be comparable when no interaction occurred between the main effects.

The apparent *in vivo* DM digestibility of each treatment was calculated according to Schneider & Flatt (1975). The metabolizable energy (ME) content of the different dietary treatments was calculated by multiplying each mean DM digestibility value with the assumed gross energy content of 18.4 MJ/kg DM and the ratio of 0.82 between digestible and metabolizable energy [ME = 0.82 (DM digestibility × 18.4)].

Statistical analyses

The data were subjected to analyses of variance according to the mixed model least squares and maximum likelihood program of Harvey (1977). In the model, dietary energy concentration, feeding level and animal effects were included, as well as dietary energy concentration × feeding level, dietary energy concentration × animal and feeding level × animal interactions. Dietary energy concentration and feeding level effects were partitioned into linear and quadratic contrasts. Feed intake was used as covariate to eliminate its effect on DM digestibility and OM retention time. The experimental unit in every analysis was the individual steer. Because period and treatment effects were inseparable, period effects were ignored.

Results and Discussion

Dry-matter intake (Table 2) decreased linearly ($P \leq 0.01$) with a decrease in feeding level as planned. However, contrary to our expectation, DM intake decreased and then increased (non-linear; $P \leq 0.01$) as the C:R ratio increased. Meissner

Table 2 Least square means for DM intake, apparent *in vivo* DM digestibility and estimated ME content[de]

Concentrate: roughage	Item	Feeding level AL	90 AL	80 AL	Row mean
80:20	Intake (kg/d)	12.8[ax]	11.4[ay]	10.1[az]	11.4[a]
	Digestibility (%)	72.9[a]	73.8[a]	76.1[a]	74.3[a]
	ME[4] (MJ/kg DM)	11.0	11.1	11.5	11.2
55:45	Intake (kg/d)	10.4[bx]	9.28[by]	8.25[bz]	9.30[b]
	Digestibility (%)	64.9[b]	65.0[b]	65.1[b]	65.0[b]
	ME[4] (MJ/kg DM)	9.80	9.80	9.82	9.80
30:70	Intake (kg/d)	10.8[bx]	9.56[by]	8.47[bz]	9.57[b]
	Digestibility (%)	55.3[c]	56.3[c]	57.1[c]	56.2[c]
	ME[4] (MJ/kg DM)	8.35	8.49	8.61	8.50
Column mean	Intake (kg/d)	11.3[x]	10.1[y]	8.95[z]	[5]**Q [6]**L [7]NS
	Digestibility (%)	64.4	65.0	66.1	[5]**L [6]NS [7]NS
	ME (MJ/kg DM)	9.72	9.80	9.93	

[x, y, z] Means in the same row and main effect with differen: alphabetic superscripts differ significantly ($P \leq 0.05$).

[a, b, c] Means in the same column and main effect with different alphabetic superscripts differ significantly ($P \leq 0.05$).

[d] Error standard deviations of the mean was respectively 0.21 and 3.13 for DM intake and digestibility.

[e] The OM content for the 80:20; 55:45 and 30:70 C:R ratios was respectively 93.57, 93.25 and 92.35%.

[4] ME value of diets based on the mean DM digestibility (see text).

[5] Diet effect.

[6] Feeding level effect.

[7] Diet × feeding level interaction.

L = linear; Q = quadratic, NS = not significant ($P > 0.05$).

* $P \leq 0.05$; ** $P \leq 0.01$.

et al. (1982) observed that OM intake increased up to 50% concentrate in the diet with *Eragrostis curvula* as roughage, after which OM intake plateaud up to 80% concentrate before it tended to decrease. According to Campher (1983) the peak level of intake of *E. curvula*-based mixed diets is influenced by the roughage particle size, and the optimum inclusion level of 25 mm hammermilled *E. curvula* is between 15 and 25%. We expected that *E. tef* would give a similar intake pattern as that observed for *E. curvula*.

Dry-matter digestibility (Table 2) tended to increase linearly ($P = 0.28$) as feeding level decreased. Observed differences were relatively small, but of the same order as noted by Hicks *et al.* (1990). Intake and digestibility are inversely related (ARC, 1980). As feed intake increases, rate of ruminal outflow may be accelerated, which causes digestibility to decrease (Owens *et al.*, 1986) because of a shorter time for exposure to digestive processes. In cattle studies, restricting intake to levels near maintenance usually increases diet digestibility (Rust & Owens, 1982; Owens *et al.*, 1986). However, effects of slight restrictions (< 15%) in feed intake of feedlot cattle on digestibility remain largely unknown (Plegge, 1987; Hicks *et al.*, 1990). According to Hicks *et al.* (1990) some benefit may be due to increased digestibility.

Eragrostis curvula has a high potential fermentability, but a slow rate of fermentation (personal communication: J.P. Pienaar, ADSRI, 1990). *Eragrostis tef* possibly has similar characteristics which appear to make it more susceptible to a depression in digestion when rapidly fermentable carbohydrates are added (Byers, 1981, as quoted by Meissner *et al.*, 1982). However, DM digestibility increased linearly ($P \leq 0.05$) as C:R ratio increased in accordance with digestibility results of Campher (1983), Meissner (1983) and Uden (1984). This linear increase in DM digestibility indicates that no associative effects occurred. This probably is due to the use of a maize by-product (hominy chop) which contains less starch than maize grain. The absence of associative effects also is supported by a parallel relationship between the ME content of diets based on tabular values and that based on DM digestibility. Meissner *et al.* (1982) observed a significant feeding level effect in OM digestibility of *E. curvula*-based diets as percentage concentrate increased. A similar feeding level effect could be responsible for the linear relationship observed in this study, due to the convex nature in which feed intake increased as C:R ratio increased. Covariance analysis, however, indicated that the influence of DM intake *per se* had no influence ($P = 0.20$) on this linear relationship. The ME content of diets based on DM digestibility (Table 2) suggested that they provided 92—93% of the ME indicated by tabular values (Table 1).

The OM retention time (Table 3) of the reticulorumen digesta, based on OM contents 2 h post feeding, decreased linearly ($P \leq 0.01$) as feeding level increased. Uden (1984) also observed that a decrease in feeding level increased the mean retention time of liquid, concentrate and hay fractions

Table 3 Least square means of reticulorumen OM content (kg), OM retention time (h) of reticulorumen digesta and rumen pH 2 h post feed[d]

Concentrate: roughage	Item	Feeding level AL	90 AL	80 AL	Row mean
80:20	OM content	8.50	8.47^{a}	9.60	8.86^{a}
	Retention time	17.7^{ax}	19.9^{ax}	24.9^{ay}	20.8^{a}
	Rumen pH	6.35^{a}	6.18^{a}	6.10^{a}	6.21^{a}
55:45	OM content	8.45	8.94^{b}	9.91	8.77^{a}
	Retention time	21.6^{abx}	25.4^{bxy}	28.4^{aby}	25.1^{b}
	Rumen pH	6.62^{a}	6.58^{a}	6.53^{b}	6.58^{b}
30:70	OM content	8.98^{x}	10.7^{by}	10.1^{xy}	9.90^{b}
	Retention time	21.9^{bx}	28.9^{by}	31.0^{by}	27.3^{b}
	Rumen pH	7.23^{b}	7.03^{b}	6.82^{b}	7.03^{c}
Column mean	OM content	8.64^{x}	9.35^{xy}	9.52^{y}	[4] NS [5]**L [6]NS
	Retention time	20.4^{x}	24.7^{y}	28.1^{z}	[4]**L [5]**L [6]NS
	Rumen pH	6.73^{x}	6.60^{xy}	6.48^{y}	[4]**L [5]**L [6]NS

[x,y,z] Means in the same row and main effect with different alphabetic superscripts differ significantly ($P \leq 0.05$).

[a,b,c] Means in the same column and main effect with different alphabetic superscripts differ significantly ($P \leq 0.05$).

[d] Error standard deviations of the mean was respectively 0.76, 2.22 and 0.22 for OM content, retention time and pH.

[4] Diet effect.

[5] Feeding level effect.

[6] Diet × feeding level interaction.

L = linear; Q = quadratic, NS = not significant ($P > 0.05$).

* $P \leq 0.05$; ** $P \leq 0.01$.

based on marker concentrations. However, Hicks *et al.* (1990) found that total tract passage rate, as calculated from Cr concentration, was not altered by limiting feed intake. In this study retention time probably over-estimated the effect of feeding level due to the feed intake pattern of the limit-fed steers; they consumed most of their feed allowance within 2 h. A decrease in feeding level increases the reticulorumen OM content (Table 3) linearly ($P \leq 0.05$) and probably gives an indication of the maximum rumen fill (personal communication: J.P. Pienaar, ADSRI, 1990).

A decrease in the C:R ratio decreased ($P \leq 0.01$) OM retention time linearly 2 h post feeding (Table 3). The slope of this relationship (−0.129) is less than the slope (−0.233) for *E. curvula* as observed by Meissner *et al.* (1982). Campher (1983) also found that the OM retention time of various roughages decreased linearly as maize meal level increased. However, OM retention time also is influenced by the type and physical form of the roughage (Campher, 1983). In contrast, Uden (1984) found that C:R ratio had no influence on the mean retention time of digesta based on marker concentrations at a particular feeding level. This suggests that the decrease in OM retention time observed in this study with an increase in the C:R ratio is due to feed intake *per se*. However, covariance analysis based on DM intake indicated that DM intake *per se* had little impact ($P = 0.43$) on this linear relationship. This probably is due to the changes in OM content of the reticulorumen which tended ($P = 0.09$) to increase non-linearly as C:R ratio decreased.

Ruminal pH and soluble rumen metabolites follow a diurnal pattern which is primarily influenced by factors such as the time, amount and frequency of feed intake as well as the type and physical form of the substrate. Ruminal parameters and metabolite concentrations reported over only part of the day may not be representative of the entire day and, thus, may not describe the mean effect of dietary changes on rumen fermentation (Robinson *et al.*, 1985). Nevertheless, they give an indication of the relative difference in fermentation rates between treatments at a specific time. Ruminal pH usually peaks just before feeding, decreases rapidly during the first 2 h post feeding (Rumsey *et al.*, 1970; Robinson *et al.*, 1985), and reach a minimum 2 h post feeding (Robinson *et al.*, 1985). Rumen pH values, determined 2 h post feeding in this study (Table 3), remained above 6.0 where no major depressing effect on structural carbohydrate fermentation is expected (Shiver *et al.*, 1986). This also reflects a relatively stable rumen environment. A decreased feed intake reduced ruminal pH linearly ($P \leq 0.05$), probably due to the starch concentration in ruminal DM which had increased non-linearly 2 h post feeding with feed intake. This decrease in pH with decreasing feeding level contrasts with results of Bath & Rook (1963) and Robinson *et al.* (1985), probably due to the feed intake pattern of our limit-fed steers; they usually consumed most of their feed allowance within 2 h post feeding. This feed intake pattern of limit-fed steers suggests that ruminal acidosis would be more prevalent when high concentrate diets are limit-fed rather than *ad libitum*-fed. A decreased C:R ratio linearly ($P \leq 0.01$) increased rumen pH, presumably due to the decreased supply of highly fermentable substrates in accordance with results of Bath & Rook (1963) and Robinson *et al.* (1985).

Table 4 Least square means of total VFA concentration and the molar percentage acetic, propionic and n-butyric acid in rumen fluid 2 h post feed[d]

Concentrate: roughage	Item	Feeding level AL	90 AL	80 AL		Row mean
80:20	VFA (mmol/100 ml)	11.0	12.4[a]	11.4[a]		11.6[a]
	Acetic acid (%)	61.2[a]	61.7[a]	58.2[a]		60.4[a]
	Propionic acid (%)	27.2[a]	27.8[a]	30.9[a]		28.7[a]
	Butyric acid (%)	10.6	9.55	10.3		10.1
55:45	VFA (mmol/100 ml)	9.48	10.2[ab]	8.84[b]		9.51[b]
	Acetic acid (%)	64.9[a]	65.9[a]	68.0[b]		66.3[b]
	Propionic acid (%)	23.0[ab]	23.6[a]	21.6[b]		22.6[b]
	Butyric acid (%)	10.8	9.85	9.47		10.0
30:70	VFA (mmol/100 ml)	8.46	8.55[b]	8.39[b]		8.46[b]
	Acetic acid (%)	70.0[b]	73.2[b]	73.1[c]		72.1[c]
	Propionic acid (%)	18.2[b]	15.5[b]	16.4[b]		16.7[c]
	Butyric acid (%)	10.8	10.2	9.52		10.2
Column mean	VFA (mmol/100 ml)	9.56	10.4	9.56	[4]**L	[5]NS [6]NS
	Acetic acid (%)	65.4	66.9	66.4	[4]**L	[5]NS [6]NS
	Propionic acid (%)	22.8	22.3	22.8	[4]**L	[5]NS [6]NS
	Butyric acid (%)	10.7	9.86	9.75	[4]NS	[5]NS [6]NS

[x,y,z] Means in the same row and main effect with different alphabetic superscripts differ significantly ($P \leq 0.05$).

[a,b,c] Means in the same column and main effect with different alphabetic superscripts differ significantly ($P \leq 0.05$).

[d] Error standard deviations of the mean was respectively 1.41, 2.44, 3.43 and 1.29 for VFA concentration, acetic, propionic and n-butyric acid.

[4] Diet effect.

[5] Feeding level effect.

[6] Diet × feeding level interaction.

L = linear; Q = quadratic, NS = not significant ($P > 0.05$).

* $P \leq 0.05$; ** $P \leq 0.01$.

The VFA concentrations increase after feeding to peak between 2 h (Robinson *et al.*, 1985) and 12 h (De Faria & Huber, 1984) post feeding, depending on the amount and type of substrate consumed. This diurnal fermentation pattern of treatments in our study may be altered due to differences in C:R ratio and feed intake pattern. A decrease in the feeding level did not influence the VFA concentration or molar percentages of acetic, propionic or butyric acids 2 h post feeding (Table 4). This contrasts with results of Bath & Rook (1963) and Robinson *et al.* (1985) who found that VFA concentrations were lower at lower intake levels. This discrepancy probably is due to the feed intake pattern of our limit-fed steers.

An increased C:R ratio linearly ($P \leq 0.05$) increased the VFA concentration which is in accordance with results of De Faria & Huber (1984) and may reflect either increased substrate availability (Estell & Galyean, 1985) or reduced dilution by saliva. The linear decrease ($P \leq 0.05$) in the molar percentage acetic acid, and the increase in propionic acid as the C:R ratio increased is in accordance with results of Bath & Rook (1963). This reflects the change in fermentation pattern as determined by type and amount of substrate (Estell & Galyean, 1985) and the species of active ruminal microbes.

In conclusion, DM digestibility increased linearly as C:R ratio increased, which indicated that no negative associative effect had occurred for extent of digestibility in the mixed diets based on maize hominy chop and *E. tef* used in this study. The absence of such an associative effect is further supported by the parallel relationship between the ME content of diets calculated from tabular values and observed DM digestibility. The linear increase in OM retention time with a decrease in C:R ratio also indicated that no associative effect occurred. The lower DM intake of the intermediate C:R ratio (55:45) was accompanied by a lower OM content in the reticulorumen, which suggests that rate of digestion was not depressed. Although a decrease in the feeding level less than 20% of *ad libitum* only tended to increase DM digestibility slightly, some benefit in diet utilization may result due to this increased digestibility. All dietary treatments produced a relatively stable rumen environment as indicated by the rumen pH 2 h post feeding. Maize hominy chop and *E. tef* hay thus can be fed in any ratio to growing and finishing cattle to achieve dietary energy densities appropriate for various levels of growth without the apparent occurrence of negative associative effects which can adversely influence their energy intake and thus growth rate.

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