determined by radioligand receptors studies (Furr *et al.*, 1987). The presence of androgen receptors in chickens and their similarities in response to exogenous androgens (5α-dihydrotestosterone > testosterone) is well established (Saartok *et al.*, 1984; Dube and Trembely, 1974; Dube *et al.*, 1975). It is likely that the inhibitory effects of testosterone on overall growth and its stimulatory effect on secondary sexual characteristics (comb) are mediated via some mechanism associated with the testosterone-receptor interaction.

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Influence of Male Broiler Breeder Dietary Energy Intake on Reproduction and Progeny Growth[1]

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ABSTRACT A study was conducted to test the effects of dietary energy intake on reproduction in genetically similar broiler breeder males and on the subsequent growth of their progeny. Fifty-nine 1-d-old pedigree broiler breeder male chicks were raised to breeding age. At 33 wk of age, 33 males were chosen and placed in one of three groups of 11 males per group and fed either 370, 330, or 290 kcal per bird per d. Each group contained both full and half brothers and had similar 6- and 33-wk mean body weights. There was a significant negative effect of decreased dietary energy intake on sperm concentration and total live sperm per milliliter of ejaculate, whereas there was no significant effect on ejaculate volume or percentage dead sperm per ejaculate.

Four groups of hens (21 wk of age) with 18 hens per group, were randomly assigned to each male dietary treatment group. Hens were artificially inseminated with 50 μL neat pooled semen from one of the three male treatment groups. There was a significant linear effect of diet on fertility, with no significant effect on hatch of fertile, hatch of eggs set, or embryonic mortality. There was no effect of sire energy intake on offspring body weights at 0, 3, or 6 wk of age. Hens were similarly artificially inseminated and sperm penetration determined for 9 consecutive d postinsemination. There was a significant quadratic relationship between sperm penetration of the perivitelline layer overlying the germinal disc and day postinsemination for each of the three male treatment groups. In addition, mean sperm penetration was 62.3, 42.9, and 6.6 holes in the germinal disc perivitelline layer for the high, medium, and low energy groups, respectively. Following 16 wk of dietary energy treatment, there was a significant linear effect of diet on mean testes weight, mean testes weight as a percentage of male body weight, and male body weight.

(*Key words*: broiler breeder, male dietary energy, reproduction, offspring growth, sperm penetration)

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INTRODUCTION

With the application of sex-separate feeding systems in broiler breeder houses, it has become increasingly important to study sex-separate management practices. Sex separate feeding helps to control BW in both male and female broiler breeders in an effort to curb fertility problems. McDaniel *et al.* (1981), found that obesity was associated with decreased fertility in broiler breeder hens, and Duncan *et al.* (1990), reported fertility problems in both overweight and underweight broiler breeder males. A significant negative relationship was reported between male BW and mating activity, and between male BW and fertility in several commercial broiler breeder flocks experiencing depressed fertility (Burke and Mauldin, 1985). These findings provide evidence of the need for nutritional management programs in broiler breeders.

Although feed restriction is necessary, Parker *et al.* (1943) reported that severe feed restriction of 42 to 72% of a control diet decreased the volume, concentration, and fertilizing capacity of semen from Rhode Island Red males, whereas Brown and McCartney (1983) reported only decreased semen volume. More recently, Sexton *et al.* (1989a) reported that broiler breeder males maintained on a severe feed restriction program experienced decreased semen volume and sperm concentration per ejaculate. Although feed restriction programs are successful in controlling BW, they also decrease the intake of protein, energy, and other important nutrients that affect reproductive characteristics.

It has been shown that a decrease in dietary protein intake has no adverse effects on semen volume or fertilizing capacity in White Leghorn males (Arscott and Parker, 1963) or in broiler breeder males (Wilson *et al.*, 1987). Low-protein diets fed to males during the growout period had no effect on semen volume and

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sperm concentration (Wilson *et al.*, 1971, 1972; Vaughters *et al.*, 1987). These reports indicate that alterations in semen characteristics due to feed restriction programs may not be due to reduced protein intake but possibly due to reduced energy intake of the males. When dietary energy intake was reduced, there was a decrease in semen volume and fertilizing capacity in White Leghorn males (Parker *et al.*, 1964). Decreases in BW, percentage of males producing semen, semen weight, total sperm per ejaculate, and sperm cell concentration were reported for caged broiler breeder males fed reduced energy levels (Sexton *et al.*, 1989b).

Interestingly, Attia and coworkers (1993, 1995) provided broiler breeder males with different levels of daily energy intake and reported a significant increase in 6-wk BW of offspring sired by males provided the high energy diets. Although this finding was evident in seven of eight trials in three experiments using two strains of broiler breeders, it is possible that males with increased genetic potential for offspring growth were inadvertently assigned to the higher energy diets. These authors also suggested that the presence of supernumerary sperm in eggs laid by hens inseminated with sperm from males fed high energy diets may somehow play a role in the increased offspring growth.

The purpose of this study was to test the effects of daily dietary energy intake in genetically similar broiler breeder males on their reproductive performance and progeny growth rate to 6 wk of age. The influence of daily energy intake on the number of supernumerary sperm penetrating the perivitelline layer overlying the germinal disc of ova fertilized *in vivo* was also determined. The issue of the effects of supernumerary sperm at the site of fertilization was also investigated in reference to dietary energy intake and offspring growth.

MATERIALS AND METHODS

Pedigree Male Growout

Fifty-nine 1-d-old pedigree (full- and half-brother) broiler breeder male chicks from one of two sires were obtained from Arbor Acres Farm, Inc.[5] These chicks consumed feed *ad libitum* and were grown to 6 wk of age under conditions similar to those which their offspring would be raised. Individual BW were obtained at hatch, and at 3 and 6 wk of age, respectively. The 6-wk BW was taken as an indicator of each male's genetic potential for 6 wk weight gain. These BW were used to try and maintain equality of the genetic potential for growth when separating the males into their dietary treatment groups. Males were individually weighed weekly until 24 wk of age, thereafter they were weighed biweekly. All pedigree chicks were vaccinated and immunized according to a prepared schedule.

[5]Arbor Acres Farm, Inc., Glastonbury, CT 06033.

Feeding and Housing

The pedigree male chicks were randomly divided into three floor pens and subjected to whole-house heating and continuous lighting. Chicks were provided *ad libitum* access to water from a nipple drinker system starting at 1 d of age. Feed was provided in floor pans for 1 wk, and from one hanging tube feeder per pen thereafter. From 1 to 28 d of age, chicks were fed The University of Georgia (UGA) Broiler Starter ration containing 3,100 kcal ME/kg, 23% CP, and 1.0% Ca. From 29 to 42 d of age, chicks were switched to the UGA Broiler Finisher ration containing 3,230 kcal ME/kg, 21% CP, and 1.1% Ca. Chicks consumed feed *ad libitum* from 0 to 6 wk of age, which allowed for comparisons of individual 6-wk BW. Although males were full fed to 6 wk of age, they were subjected to a feed restriction program designed with the intent of allowing males to gradually arrive at or near the Arbor Acres Farms target weight for commercial 24-wk-old broiler breeder males. At 10 wk of age, the males were moved into a dark house [8 h light (L):16 h dark (D)] and randomly redivided into three floor pens. Water was available from one hanging bell waterer per pen and feed from two hanging tube feeders per pen. At 24 wk of age, the 35 remaining males were moved into individual male breeder cages and subjected to a 16L:8D photoperiod in a temperature-controlled house for the remainder of the study. Water was available from nipple drinkers and birds were individually fed the UGA Breeder diet (2,915 kcal ME/kg, 15% CP, and 3% Ca) for maintenance until initiation of the dietary treatments.

Experimental Breeder Management

At 33 wk of age, the remaining 35 pedigree males were weighed and, based upon genetic relationship to each other and their 6- and 33-wk BW, 33 males were divided into three groups of 11 males per group. Each of the three dietary treatment groups were similar in their respective BW both at 6 and 33 wk of age and contained either full sibs (three per group), or half sibs (eight per group).

The three groups of males were randomly assigned to either the high (H; 370 kcal per bird per d), medium (M; 330 kcal per bird per d), or low (L; 290 kcal per bird per d) energy diet and fed 120 g/d of their respective diet. The rations for each diet are shown in Table 1. Each male treatment group of birds was subdivided into three subgroups of three to four males per subgroup for statistical analysis of semen characteristics.

Two-hundred and sixteen 21-wk-old Arbor Acres broiler breeder hens were obtained from a commercial source and randomly assigned to individual cages and housed under the same confinement conditions as the males. Hens were divided into 12 groups of 18 hens each to be used as replicates for each of the three male treatment groups (four hen replicate groups per male treatment group). All birds were subjected to a 16L:8D photoperiod and were fed the UGA Breeder diet as

TABLE 1. Composition of the experimental rations

Ingredients and composition	Dietary energy allotment 290 kcal/d	330 kcal/d	370 kcal/d
	(%)		
Yellow corn	27.74	54.59	81.38
Wheat shorts	68.81	35.94	2.85
Soybean meal (48%)	0.00	5.91	12.10
Limestone	2.14	2.04	1.94
Dicalcium phosphate	0.56	0.77	0.98
Salt (NaCl)	0.45	0.45	0.45
Vitamin mixture[1]	0.25	0.25	0.25
Mineral mixture[2]	0.05	0.05	0.05
Total	100	100	100
Calculated composition			
ME, kcal/kg	2,417	2,750	3,083
Crude protein	13.80	13.60	13.50
Methionine	0.24	0.25	0.26
TSAA	0.53	0.50	0.48
Lysine	0.61	0.60	0.60
Calcium	1.00	1.00	1.00
Available P	0.30	0.30	0.30
Ether extract	4.22	3.79	3.34
Crude fiber	5.29	3.88	2.46

[1]Vitamin mixture provides in milligrams per kilogram of diet: vitamin A (as all-*trans*-retinyl acetate), 5,500 IU; vitamin E (all *rac*-α-tocopherol acetate), 11 IU; menadione (as menadione sodium bisulfite), 1.1 mg; cholecalciferol, 1,100 IU; riboflavin, 4.4 mg; Ca pantothenate, 12 mg; nicotinic acid, 44 mg; choline chloride, 191 mg; vitamin B_{12}, 6.6 μg; vitamin B_6, 2.2 mg; thiamine (as thiamine mononitrate), 2.2 mg; folic acid, 0.55 mg; d-biotin, 0.11 mg.

[2]Trace mineral mixture provides in milligrams per kilogram of diet: Mn, 60; Zn, 50; Fe, 30; Cu, 5; I, 1.50; Se, 0.3.

previously described to maintain their BW at or near the target weight as outlined by the primary breeder.

Semen Characteristics

Semen was collected on a weekly basis using the abdominal massage method (Burrows and Quinn, 1937) in order to keep them trained and in production. Semen was collected for analysis of individual semen parameters from each male at 38, 42, and 46 wk of age (5, 9, and 13 wk following initiation of the dietary treatment), respectively. The volume of each ejaculate was recorded and the sperm cell concentration determined by packed cell volume (Maeza and Buss, 1976). The percentage dead sperm in each sample was determined using the fluorometric method (Bilgili and Renden, 1984; McDaniel *et al.*, 1995) and the total live sperm cell concentration calculated by multiplying the sperm cell concentration by the percent live sperm from each individual sample.

Fertility and Hatchability

At 36 and 44 wk of age (3 and 11 wk of study), hens were artificially inseminated with 50 μL neat pooled semen from males fed either the H, M, or L energy diets. The actual number of live sperm inseminated into each group of hens in the first insemination period was 2.15, 1.67, and 2.15×10^8 per hen for the H, M, and L energy male groups, respectively; while the actual live sperm numbers inseminated in the second insemination period was 2.00, 2.02, and 1.69×10^8 per hen, respectively. Eggs were collected daily for 9 consecutive d following insemination and stored in an egg storage room at 15.5 C and 70% relative humidity. All eggs were set 10 d following insemination in Natureform Incubators[6] at 37.6 C and 54% relative humidity. Eggs were candled following 10 d of incubation to determine fertility and eggs that appeared infertile or dead were broken open for macroscopic inspection of the blastodisc to identify the stage of development of any early-dead embryos (Hamburger and Hamilton, 1951). Embryonic mortality was recorded as either early- (1 to 7 d) or late-dead embryos (18 to 21 d; including unhatched pips) for analysis purposes. Fertile eggs were further incubated to determine the percentage hatch of fertile and percentage hatch of eggs set for each male treatment group for each of the two insemination periods.

Sperm Penetration

At 48 wk of age (15 wk of study), hens were artificially inseminated with 50 μL neat pooled semen from males fed either the H, M, or L energy diets (2.31, 1.90, and 1.22×10^8 total sperm per hen, respectively). Eggs were collected daily for 9 consecutive d postinsemination and labeled by group and day collected. Sperm penetration of the

[6]Model Mini NMC2000, Natureform Incubators, Inc., Jacksonville, FL 32202.

TABLE 2. Body weight of male broiler breeders fed different daily dietary energy allotments[1]

Dietary energy allotment	n	Body weight		
		6 wk	33 wk	48 wk
(kcal/d)		(g)		
370	11	2,412	5,912	5,889
330	11	2,418	5,939	5,213
290	11	2,400	5,937	4,620
SEM		71.0	103.0	120.0
Regression[2]		0.91	0.87	0.0001

[1]Six-week body weights were made following full feeding, 33-wk body weights were made following feed restriction program and prior to placing males in dietary energy groups, 48-wk body weights were taken after 16 wk on dietary energy feeding program. All values represent the means of 11 individual body weights.

[2]Probability that the linear regression coefficients relating sire body weight to sire energy allotment were different than zero.

perivitelline layer overlying the germinal disc was determined in the laid eggs as described by Bramwell *et al.*, (1995).

Progeny Performance

Chicks obtained when collecting the fertility and hatchability data (3 and 11 wk of study), were grown out to determine the effects of sire's dietary energy intake on broiler offspring growth. Up to 192 unsexed chicks were randomly selected from all chicks hatched from each of the male treatment groups for each growout period. Day-old chicks were weighed, wing-banded, vaccinated for Marek's disease, and randomly divided into each of 24 pens. Chicks from each male treatment group were raised co-mingled with chicks from each of the other male treatment groups in each of the 24 replicate pens. Each pen was equipped with nipple drinkers and one hanging tube feeder. The temperature was controlled by whole-house heating. Chicks ate *ad libitum* the UGA Broiler Starter diet for 4 wk and the UGA Broiler Finisher diet for the last 2 wk as described for the sire growout feeding program. Individual chick BW were obtained at 3 (21 d) and 6 (42 d) wk of age, with the sex determined while collecting the 6-wk BW. Chicks from a given treatment and sex were used to obtain a single mean chick BW value for each age, treatment, and sex within each of the 24 replicate pens.

Testes

After the conclusion of all insemination and semen collection periods, BW was measured for each of the 49-wk-old pedigree males (16 wk of study). Males were killed by cervical dislocation and the testes were removed from seven randomly chosen males per treatment group and weighed. Testes weights were expressed in grams and in terms of percentage BW for each of the male treatment groups, respectively.

Statistical Analyses

Linear regression analyses were performed on all data to obtain the probability that the slope of the regression lines due to diet were significantly different from zero. The ANOVA procedure was also used on all data to obtain the SEM values displayed in the tables. For semen characteristics and sperm penetration, the subgroups of males (three subgroups per male treatment, with each subgroup containing three or four males each) were used as the experimental units of measure for each of the male energy groups, respectively. For semen characteristics, there was a split-plot in time, regression coefficients of which were analyzed along with the interaction term of diet and time. The ANOVA procedure was also used on sperm penetration to separate the overall mean sperm penetration values using Student-Newman-Keuls multiple range test. Linear and quadratic regression coefficients were tested for sperm penetration values over day postinsemination by diet, with the solution statement (SAS Institute, 1985) used to compare the slopes of the lines between the H, M, and L diets. For fertility and hatchability data, there was a split-plot in time with the four hen groups per male treatment used as the experimental units. For offspring BW values, a single mean value for each age was obtained from all chicks for each sex and sire treatment within each pen. Mean values from each of the 24 pens were then used as the experimental units of measure. For testes weight, testes weight as a percentage of male BW, and male BW at 6, 33, and 48 wk of age, the individual male values were used as the experimental units in the regression analysis. All tests were performed using SAS® software (SAS Institute, 1985).

RESULTS

Although all groups experienced a decrease in BW throughout the course of the 15-wk study, there was a significant effect of diet on 48-wk male BW (Table 2). During the course of the study there was no mortality in any of the three male dietary treatment groups. The percentage of males producing semen decreased from 100% in all dietary treatment groups in the first collection period, to as low as 36% in the L group in the third collection period (Table 3).

TABLE 3. Semen characteristics of broiler breeder males fed different daily energy allotments[1]

Dietary energy	Age of male	Semen production[2]	Ejaculate volume	Total sperm count	Dead sperm	Total live sperm count
(kcal/d)	(wk)	(%)	(mL)	(× 10^9/mL)	(%)	(× 10^9/mL)
370	38	100.0	0.42	4.61	17.4	3.93
370	42	100.0	0.33	4.63	10.3	4.10
370	46	81.8	0.26	5.19	8.4	4.77
330	38	100.0	0.37	4.65	21.5	4.38
330	42	72.7	0.33	4.20	16.5	3.61
330	46	63.6	0.28	4.01	12.0	3.54
290	38	100.0	0.30	5.41	16.9	3.94
290	42	54.5	0.27	3.06	12.0	2.86
290	46	36.3	0.22	2.65	6.3	2.50
			Probability			
Regression analyses[3]						
Diet			0.12	0.003	0.92	0.002
Time			0.02	0.06	0.0003	0.24

[1]Parameters measured represent the mean values from three groups of males per dietary treatment group with three or four males per subgroup (n = 3).

[2]Percentage males producing semen out of 11 males in each dietary treatment group, respectively.

[3]Probability that the linear regression coefficients relating the semen parameters measured to diet, time, or the interaction term of diet and time were different than zero.

There was a significant diet by time interaction on sperm concentration and percentage live sperm ($P < 0.003$) with no significant interaction effect on ejaculate volume or percentage dead. Although there was no significant linear effect of age on total sperm count from all males combined, the effect of time was significant for males fed the M ($P < 0.03$) and L ($P < 0.01$) diets (Table 3). There was a significant linear effect of age on percentage dead sperm per ejaculate ($P < 0.0003$), as these values decreased to 8.4, 12.0, and 6.3% for the H, M, and L groups, respectively. From all males combined, there was a significant main effect of diet on the total sperm count ($P < 0.003$) and the total live sperm count per milliliter of ejaculate ($P < 0.002$) with no linear effect of diet on ejaculate volume or percentage dead sperm.

There was a significant overall linear effect of diet on fertility ($P < 0.003$), with no significant effect on hatch of fertile eggs, or hatch of eggs set (Table 4). There was also no interaction effect of diet and day postinsemination for any of the three reproductive characteristics measured ($P > 0.6$; data not shown). There was no significant effect of diet or day postinsemination on embryonic mortality (early- or late-dead), with mean treatment group values ranging from 8.7 to 4.3% dead embryos (data not shown).

There was a significant diet by day postinsemination interaction on sperm penetration ($P < 0.0001$) with the main effect of diet and day postinsemination also significantly affecting sperm penetration ($P < 0.0001$). There was a quadratic relationship between sperm penetration and day postinsemination for the H, M, and L energy diets (Figure 1). The linear and quadratic slopes of the lines from all three diets, were significantly different due to dietary energy treatment. When comparing the quadratic slopes for sperm penetration over day postinsemination in the H and M male groups, the H ($P < 0.02$) and M ($P < 0.04$) males were significantly different than the L males. However, there was no significant difference in the slopes of the lines between the H and M male groups ($P \geq 0.7$). The intercepts for all three quadratic lines were also significantly different for the H, M, and L energy groups (207.7, 155.5, and 30.8, respectively, $P < 0.0001$). When comparing overall means for sperm penetration, there were significant

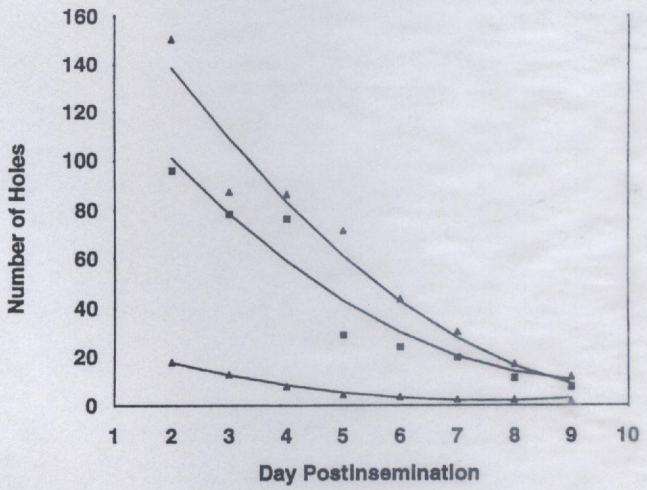

FIGURE 1. Sperm penetration holes in eggs laid for each day postinsemination for each of the three dietary energy treatment groups. There was a quadratic relationship between sperm penetration and day postinsemination for the High (△; $y = 207.7 - 38.3x + 1.8x^2$, $r^2 = 0.93$, $P < 0.003$), Medium (■; $y = 155.5 - 30.5x + 1.6x^2$, $r^2 = 0.90$, $P < 0.005$), and Low (▲; $y = 30.8 - 7.6x + 0.5x^2$, $r^2 = 0.86$, $P < 0.0001$) energy groups, respectively. Values represent the replicate means from three groups of hens (18 hens per group) for each male treatment group (n = 3).

TABLE 4. Reproductive characteristics of broiler breeder males fed different daily energy allotments from two separate inseminations

Dietary energy allotment	Fertility			Hatch of fertile eggs			Hatch of eggs set		
	36 wk[1]	44 wk[1]	$\bar{x}$	36 wk	44 wk	$\bar{x}$	36 wk	44 wk	$\bar{x}$
(kcal/d)	(%)								
370	75.5	78.6	77.1	81.6	86.5	84.1	62.0	67.1	64.6
330	83.1	70.3	76.7	84.4	85.8	85.1	69.7	62.0	65.9
290	73.9	64.5	69.2	84.5	92.1	88.3	62.9	59.2	61.1
SEM	4.91	8.96	5.50	3.65	4.17	2.55	5.67	8.96	5.63
Regression[2]	0.65	0.001	0.003	0.43	0.11	0.06	0.84	0.02	0.22

[1]Values from each insemination represent replicate means from four groups of 18 hens per group from eggs laid for 9 consecutive d following insemination (n = 4).

[2]Probability that the linear regression coefficients relating reproductive characteristics to sire energy intake were different than zero.

differences between each of the H, M, and L dietary energy groups (62.3, 42.9, and 6.6 holes per germinal disc perivitelline layer, respectively; SEM = 1.22).

There were no significant linear regression coefficients relating offspring 3- and 6-wk BW and sires' dietary energy intake for either the male (Table 5) or female (Table 6) chicks produced. There was, however, a significant linear effect of sire energy intake on hatch weight from male chicks in Growout 1 and in female chicks in both growouts, although the overall regression coefficient for each was not significant ($P > 0.15$, and 0.94, respectively). When separating the overall mean values, there was no significant difference in chick hatch weight due to sex ($P > 0.21$); however, at 3 and 6 wk of age, mean BW was different between the sexes ($P < 0.0001$). Also, decreased dietary energy intake had a significant linear effect on testes weight ($P \leq 0.01$), and testes weight as a percentage of BW ($P \leq 0.03$; Table 7). The mean percentage change in male BW over the course of the study for the H, M, and L groups were –0.5% (range = 13.7 to –11.9%), –12.0% (6.5 to –25.8%), and –21.5% (–1.4 to –34.1%), respectively. The mean testes weight loss was 54.9 and 65.5% for the M and L groups as compared to the H group males.

DISCUSSION

The levels of dietary energy chosen for this study were similar to those used by Attia and coworkers (1993, 1995). The latter study revealed that when males near 4 kg in BW were fed 300 kcal per bird per d dietary energy, they were able to maintain their respective BW over the length of the study (~ 75 kcal/kg BW). In this study, males had initial mean BW of approximately 5.9 kg (Table 2) and 370 kcal dietary energy intake was needed per d to maintain their respective BW (63 kcal/kg BW per bird per d). This value is similar to that found by Sexton (1989b), who reported that 55 kcal/kg BW was sufficient to maintain BW, and much lower than that found in earlier studies by McCartney and Brown (1980) and Brown and McCartney (1983, 1986), who suggested caloric needs of 105, 81, and 95 kcal/kg BW per d. Because of the large size of males used in this study, those males fed the M and L diets lost weight over the 16-wk diet treatment period, indicating that daily energy intake was insufficient for their respective maintenance requirements. As previously mentioned, it has been shown that a decrease in male BW has been associated with fertility problems in broiler breeders

TABLE 5. Body weight of male broiler chicks sired by males fed different daily energy allotments[1]

Chick age	Sire dietary energy allotment				
	290 kcal/d	330 kcal/d	370 kcal/d	SEM	Regression[2]
(d)	(g)				
Hatch 1					
1	36.7	37.2	37.9	0.31	0.01
21	682.0	663.0	688.0	6.7	0.54
42	2,306	2,237	2,314	23.0	0.83
Hatch 2					
1	40.3	39.2	40.4	0.28	0.91
21	673.0	678.0	682.0	7.5	0.42
42	2,260	2,149	2,227	23.0	0.35
Overall					
1	38.6	38.3	39.2	0.21	0.18
21	677.0	671.0	685.0	5.1	0.31
42	2,283	2,192	2,269	15.0	0.61

[1]Values represent the means of all male chicks (from 2 to 10 chicks per pen), from each sire treatment insemination period. Chicks were randomly placed in 23 pens (Hatch 1; n = 23) or 24 pens (Hatch 2; n = 24).

[2]Probability that the linear regression coefficients relating male offspring body weight to sire energy allotment were different than zero.

TABLE 6. Body weight of female broiler chicks sired by males fed different daily energy allotments[1]

Chick age	Sire dietary energy allotment				
	290 kcal/d	330 kcal/d	370 kcal/d	SEM	Regression[2]
(d)	(g)				
Hatch 1					
1	36.5	36.8	37.6	0.32	0.02
21	630.0	620.0	627.0	5.8	0.71
42	1,967	1,916	1,971	17.0	0.87
Hatch 2					
1	40.6	39.5	39.4	0.23	0.002
21	614.0	598.0	618.0	8.3	0.72
42	1,895	1,841	1,895	25.0	0.98
Overall					
1	38.6	38.1	38.6	0.20	0.95
21	622.0	609.0	622.0	5.7	0.93
42	1,930	1,878	1,932	16.0	0.92

[1]Values represent the means of all female chicks (from 2 to 10 chicks per pen), from each sire treatment insemination period. Chicks were randomly placed in 23 pens (Hatch 1; n = 23) or 24 pens (Hatch 2; n = 24).

[2]Probability that the linear regression coefficients relating female offspring body weight to sire energy allotment were different than zero.

(Harris *et al.*, 1984; Burke and Mauldin, 1985; Duncan *et al.*, 1990).

Throughout the 16-wk dietary energy treatment period, the percentage of males producing semen decreased in all groups, although more drastically in the M and L energy groups (Table 3). This result supports observations reported by Harris *et al.* (1984), in which the percentage of males producing semen decreased with increasing age and with a decrease in male BW. The decrease in the volume of ejaculate over time supports the results of Sexton *et al.* (1989b) and Lake (1989), who reported that as males aged their ejaculate weight was decreased. Even though the overall linear effect of age on total sperm concentration was not significant, there was a significant decrease in sperm concentration with increased time on the M and L dietary treatments (M, $P < 0.03$; and L, $P < 0.01$). These results support those reported by Sexton *et al.* (1989b) that daily dietary energy intake below the basal level would result in decreased sperm concentration per milliliter of semen.

Interestingly, in conjunction with the decrease in sperm concentration in the M and L groups over time, there was also a significant decrease in the percentage of dead sperm per ejaculate in all three treatment groups. Although the number of total live sperm per milliliter of ejaculate was still reduced in the L males, with the decline in percentage of dead sperm, the change over time was not quite as severe (Table 3). Bramwell *et al.* (1996) reported that there was an increase in fertility of old males as compared to young males when inseminated with equal numbers of total spermatozoa. The decrease in percentage dead sperm over time may offer an explanation for the higher fertility obtained in older males in the previously mentioned study.

With decreasing levels of dietary energy, there was a significant decrease in overall fertility from the two insemination periods (Table 4). This decrease, however, cannot be related entirely to the number of sperm inseminated per hen from semen collected from each of the male treatment groups. Based upon the mean number of live sperm inseminated from each of the male groups over both insemination periods (2.1, 1.8, and 1.9 $\times 10^8$ sperm per hen for the H, M, and L male groups, respectively), a significant difference in fertility would not be expected. Therefore, the low daily energy intake may have somehow impeded the fertilizing capacity of sperm from the L males. The hatchability data obtained was consistent with Attia *et al.* (1995), with no significant effect of diet on overall hatchability.

Sperm penetration values were consistent with what could be expected for the doses of sperm inseminated as reported by Bramwell *et al.* (1995). Because a constant volume of neat pooled semen from each male group was inseminated into the hens, the concentration of sperm was not consistent across groups. Although sperm concentration per milliliter of semen was decreased in the L male group, the decrease in mean sperm penetration from eggs laid by hens assigned to this

TABLE 7. Testes characteristics of male broiler breeders fed different daily dietary energy allotments[1]

Dietary energy allotment	n	Number in production	Testes weight	
(kcal/d)			(g)	(% BW)
370	7	5	25.9	0.44
330	7	3	11.7	0.22
290	7	2	8.9	0.20
SEM			4.31	0.07
Regression[2]			0.01	0.03

[1]Values represent weights of both testes removed from seven randomly selected males from each male dietary treatment group (n = 7).

[2]Probability that the linear regression coefficients relating testes characteristics to sire energy allotment were different than zero.

group was even greater than might be expected. The complete explanation for this is unclear, but the males' low daily dietary energy intake may somehow affect sperm motility and sperm storage within the hen. This would result in fewer sperm available for penetration of the perivitelline layer at the site of fertilization. In addition, the L dietary energy treatment may depress the ability of sperm cells to penetrate the perivitelline layer. The difference in the quadratic regression slopes between the H and M groups and the L group also indicates that other factors affected sperm penetration beyond the effect of sperm concentration inseminated, such as sperm storage within the hen. However, additional studies that measure sperm storage and sperm presence at the site of fertilization are needed to confirm these suggestions.

As stated previously, the L energy diet resulted in a significant decrease in the number of males in semen production for that treatment group. Consequently, only two offspring growouts were completed. However, there was no significant linear effect of diet on offspring BW at either 3 or 6 wk of age. This result is in contrast to that reported by Attia and coworkers (1993, 1995), who reported that increased dietary energy resulted in a significant increase in offspring BW in seven out of eight growth trials. They suggested that a possible cause for the increased offspring BW might be related to an increase in supernumerary sperm present at the site of fertilization.

The occurrence of increased sperm penetration at the site of fertilization (germinal disc area) has been well documented (Howarth and Digby, 1973; Bakst and Howarth, 1977; Bramwell and Howarth, 1992). Although physiological polyspermy is a common occurrence in avian species, the exact role of these "extra" sperm is unknown. In this study, mean sperm penetration of the perivitelline layer overlying the germinal disc was found to be significantly influenced by male daily energy intake. Although there were differences in the intercepts of the slopes of the regression lines over days postinsemination (Figure 1) and differences in mean sperm penetration between the dietary treatment groups, there was no significant difference in offspring BW due to diet. These data, from genetically equivalent males, are in contrast to the suggestion of Attia and coworkers (1995) that the degree of polyspermy may influence the offspring BW at 6 wk of age. However, the sperm penetration values reported here were determined at the conclusion of the study, whereas the growout data was obtained from inseminations during the course of the study. Therefore, the actual sperm penetration numbers reported are probably lower than would have been expected at the time the eggs were fertilized to produce chicks.

Another possible explanation for the increased BW in response to increased energy intake suggested by Attia *et al.* (1995) was through chance assignment of males with increased genetic potential for weight gain to the high energy groups. This possibility, however, seems remote considering their replication over growouts and experiments. To test the possibility of chance assignment of "superior" males to the higher energy groups, full- and half-brother sires (assessed as genetically equivalent by group) were used in this experiment with no effect on offspring BW.

Based upon results reported here, there is a more likely explanation for the difference in mean offspring BW between sires fed high or low energy levels reported by the previous authors. It can be assumed that there is a given amount of variation between males within a group in their genetic makeup for offspring growth. Through random assignment of males to dietary energy groups, this genetic variation would most likely remain within each assigned treatment group of males. Assuming that the males that have increased genetic potential for offspring growth may also be the larger birds in body size and weight, they would be affected by the low energy diets earlier in the treatment period and to a greater degree than the smaller males. If this were true, it is likely that the larger males would be the first to go out of semen production and would contribute little, from a genetic standpoint, to the production of offspring from that male treatment group. The larger males in the higher daily energy intake groups would not be so affected by diet and thus would continue to produce semen and contribute genetically to the production of offspring. In this scenario, offspring BW would actually be reduced in the lower daily energy groups as compared to the sire groups that received adequate levels of dietary energy. The use of genetically similar males in this study eliminated such a possibility and more accurately reflected the effects of diet on the reproduction capabilities in these full and half brother broiler breeder males. In conclusion, varying levels of daily dietary energy intake by full- and half-brother sires had no significant effect on mean offspring BW at 3 or 6 wk of age.

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