Protein and Energy Relationships in the Diet of the American Alligator (*Alligator mississippiensis*)[1]

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ABSTRACT First-year alligators (*Alligator mississippiensis*) averaging 377–857 g body weight were fed diets containing various levels of protein, fat and carbohydrate. In experiment 1, nine diets arranged in a centrally rotatable composite design contained 0–36% extruded corn and 4–20% total fat. Response surface analysis predicted maximum responses in performance criteria at 6.3–18.8% corn and 15.8–27.4% fat. Corn inclusion at up to 27–36% of diet resulted in equal or improved performance compared to carbohydrate-free diets of equal fat content. Energy digestibility averaged 84.3%. Protein digestibility averaged 86.7%. Maximum responses in performance criteria were predicted at 42.5–48.7% digestible protein and 4367–4421 kcal/kg digestible energy. In two additional experiments, alligators were either fasted or fed for various numbers of days/week. Carbohydrate-supplementation of high protein diets led to equal or significantly improved performances. Performance was maximized by feeding the alligators 5–6 d/w. Regression of body weight changes against energy and protein intake yielded estimates of daily maintenance requirements of 5.7–8.4 kcal and 0.49–0.89 g protein/kg live body weight. Dietary fat and carbohydrate in the forms and amounts fed to young alligators were well-utilized. Optimal digestible energy:crude protein ratios (8.2–10.9:1 kcal/g protein) were similar to those of other aquatic ectotherms of equal size. *J. Nutr.* 120:775–785, 1990.

INDEXING KEY WORDS:

- *alligator* • *carbohydrate* • *fat*
- *energy requirement* • *protein requirement*
- *energy-protein relationship*

The nutrition of American alligators (*Alligator mississippiensis*) is gaining increased attention because farming of this species for its hide and meat is an established and growing agribusiness in the southeastern United States. Furthermore, a number of dietary peculiarities have been attributed to this carnivorous reptile, and their elucidation would be of interest to nutritionists interested in the feeding of carnivorous and/or cold-blooded animals. Specifically, alligators have been reported to be unable to digest vegetable protein or carbohydrates (1) and to exhibit reduced growth in response to dietary fat, even when fat content (6.7% of dry matter) is relatively modest (2). This leaves only animal protein as a major dietary energy source in practical diets. Captive alligators are indeed able to prosper on very high (> 70%) meat protein, carbohydrate-free, fat-free diets (2). Under these dietary conditions, energy for growth and maintenance must be derived from protein, which may be energetically inefficient. Furthermore, very high protein diets are not practical because of cost and manufacturing considerations. Therefore, in this study we have attempted to characterize the reported limitations of alligators with regard to dietary energy sources.

From the standpoint of experimental design, carbohydrate-free, low fat, high protein diets provide little latitude in studies of relationships between protein and energy. Recently, we (3) have demonstrated that hatchling alligators benefit from and apparently do utilize some dietary carbohydrate. Furthermore, fat was readily digested and absorbed. Dilution of high protein diets with up to 16.6% fat improved body weight gains and feed efficiency. In the present experiments with 6- to 10-mo-old alligators, we confirm that dietary fat and carbohydrates, within limitations, enhance performance. Additionally, formulation of diets using these nonprotein energy sources has made possible this investigation of the protein and energy relationships of this species.

[1]Supported by a grant from the Louisiana Department of Wildlife and Fisheries, by State and Hatch funds allocated to the Georgia Agricultural Experiment Stations of the University of Georgia, and by a contract (DE-AC09-76SR00-819) between the U.S. Department of Energy and the University of Georgia.

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0022-3166/90 $3.00 © 1990 American Institute of Nutrition. Received 24 May 1989. Accepted 29 December 1989.

METHODS

Animals and housing. Alligators used in these experiments were hatched from eggs artificially incubated at Rockefeller Wildlife Refuge (Grand Chenier, LA) according to the methods of Joanen and McNease (4) and were transported immediately to University of Georgia facilities by automobile. Alligators were used in one or two other nutrition experiments (3, 5) prior to use in the present studies. Animals from treatment groups of previous experiments were evenly distributed throughout new treatments. Between experiments (3–16 wk), animals were fed vitamin-supplemented ground meat or a formulated diet considered to be adequate based on experience in our laboratory.

Experiment 1 was conducted for 15 wk. Animals were housed in rectangular, 0.6-m deep, covered, fiberglass-lined tanks with a total living area of ~1 m^2. This space was divided into dry and water (4–8 cm deep) areas in a 1:2 ratio, respectively, as recommended by Joanen and McNease (6). Tank water was part of a heated (29–32°C) recirculating water system in which water flowed 20 of every 60–120 min. Housing and physical layout have been further described elsewhere (7). Each tank was partitioned into two identical pens of ~0.5 m^2, to which dietary treatment groups were randomly assigned. Four alligators were allocated to each of these groups (replicates) on a random basis with the constraints that within-pen variation in individual body weight (recorded ± 0.5 g) was minimized, and initial average body weight (377 g) was not significantly different between pens or treatments. Animals from each pen were also weighed (± 0.5 g) collectively after 8 and 15 wk. Total length was measured (± 0.5 mm) only at the end of the study but was known to be similar for all treatment groups at the beginning of the experiment based on previous records.

Experiments 2 and 3 are conducted for 5 and 4 wk, respectively. Replicate groups consisted of tanks of two alligators. Allocations to experimental groups were made as described previously. Initial body weights averaged 506 g for experiment 2 and 857 g for experiment 3. Animals were housed in 0.6 m × 0.6 m opaque plastic tanks filled with water to a depth of 12 cm. Water temperature was allowed to fluctuate with room temperature, which varied between 29 and 32°C. A 10 cm × 20 cm plastic platform elevated above water level served as a feeding station.

In experiment 1, tanks were washed and refilled with warm (27–30°C) water after each feeding. In experiments 2 and 3, all tanks were cleaned and refilled with warm water 6 and 7 d/w, respectively. In experiment 1, animals were maintained in total darkness except during feeding and cleaning. In experiments 2 and 3, animals were maintained on a 14L:10D photoperiod.

Diets and feeding schedules. A high protein, low fat, carbohydrate-free diet was formulated. Fat and/or a carbohydrate source was substituted to various degrees for the protein component of the diet (**Table 1**). Dietary calcium and phosphorus were maintained at ~1.0% and 0.5%, respectively, through additions of limestone and dicalcium phosphate. Gelatin and high viscosity carboxymethyl cellulose (Sigma Chemical, St. Louis, MO) were included as binders. Water was added to the air-dry diet (Table 1) to form a moistened cake (32–50% moisture), which was frozen for up to 1 mo. Prior to feeding, the diet was warmed to ~28°C and chopped into bite-size pieces.

In experiment 1, animals were fed three times weekly. In experiment 2, alligators were either fasted or fed 2, 3, 5 or 6 d/wk. In experiment 3, animals were either fasted or fed 1, 3, 5 or 7 d/wk. Feed was offered for 1 or 2 h per feeding. Animals that were fed only 1 or 2 d weekly occasionally consumed all feed offered. Others did not, however, and were judged to have reached satiation. Dry matter consumption was calculated by weighing feed offered and uneaten, subtracting, and adjusting for moisture.

Analytical methods. Alligators deposit feces as semi-dry pellets, usually in water. Intact fecal pellets were removed and frozen within 1–2 h after tank cleaning in order to minimize contamination and leaching. Leaching of solubles from feces into water was considered to be a potential source of error. However, in other experiments (Staton et al., unpublished data), it was determined that fat and protein digestibilities estimated with feces remaining in water for up to 6 h were biased upward by only 2% and 1%, respectively. This was an acceptable margin of error, considering the very high digestibility coefficients expected. Feces were freeze-dried prior to analysis. Chromic oxide was included at 0.1% as a dietary marker. Feed and fecal chromic oxide were determined by the method of Brisson (8). Dietary and fecal crude protein levels were determined using the Kjeldahl nitrogen method (9). Gross energy was measured in an adiabatic bomb calorimeter (Parr Equipment, Moline, IL). All determinations were performed in duplicate. Digestible protein (DP) and digestible energy (DE) were calculated by multiplying the analyzed values of dietary crude protein and gross energy by their respective digestive coefficients (10).

Digestibility of protein and energy was determined with a standard equation (11):

$$\text{Percent nutrient digestibility} = 100 - 100 \times \frac{(\%\ Cr_2O_3 \text{ in food})(\%\ \text{nutrient in feces})}{(\%\ Cr_2O_3 \text{ in feces})(\%\ \text{nutrient in feed})}$$

Experimental design and statistical analyses. In experiment 1, a central composite rotatable design (12) was used with corn and fat as dietary variables ranging from 0–36% and 4–20%, respectively. The central dietary treatment (12% fat; 18% corn) was replicated six times, and peripheral treatments were replicated three

TABLE 1

Composition of experimental diets

	Experiment 1									Experiment 2		Experiment 3	
Ingredient	1	2	3	4	5	6	7	8	9	Carbo-hydrate	Protein	Carbo-hydrate	Protein
							%						
Protein mixture[1]	45.72	57.28	45.33	72.71	64.50	55.69	83.15	71.23	82.73	52.25	67.25	63.25	78.25
Chicken liver dry matter[2]	—	—	—	—	—	—	—	—	—	10.00	10.00	—	—
Fat mixture[3]	8.83	2.97	14.62	0.44	8.75	17.06	2.90	14.52	8.72	—	—	—	—
Poultry oil	—	—	—	—	—	—	—	—	—	12.00	9.20	12.0	12.0
Extruded corn	36.00	30.60	30.60	18.00	18.00	10.00	5.40	5.40	—	—	—	15.0	—
Corn dextrin[4]	—	—	—	—	—	—	—	—	—	16.00	4.00	—	—
Gelatin	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Carboxymethylcellulose[5]	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Limestone	1.50	1.50	1.50	1.70	1.60	1.60	1.80	1.70	1.80	2.00	2.00	2.00	2.00
Potassium carbonate	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40
Dicalcium phosphate	1.20	0.90	1.20	0.40	0.60	0.90	—	0.40	—	1.00	0.80	1.00	0.80
Sodium chloride	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Vitamin premix[6]	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Trace mineral premix[7]	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20
Chromic oxide	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
Selenium premix[8]	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
<u>Analysis</u>													
Crude protein, %[9]	41.4	50.1	40.6	61.4	54.6	47.8	68.6	59.1	67.9	48.4	61.7	49.8	59.5
Fat, %[9]	12.0	6.4	17.6	4.0	12.0	20.0	6.4	17.6	12.0	15.7	13.2	14.8	14.8
Carbohydrate, %[9,10]	26.2	22.2	22.2	13.1	13.1	13.1	3.9	3.9	—	16.0	4.0	10.7	—
Gross energy, *kcal/kg*[11]	4824	4669	5085	4734	5051	5266	4982	5331	5283	5424	5445	5310	5540
kcal/g protein	11.7	9.3	12.5	7.7	9.25	11.0	7.3	9.0	7.8	11.2	8.8	10.7	9.3

[1]44.6% casein, 33.9% blood meal, 20.9% feather meal, 0.36% arginine HCl, 0.24% DL-methionine.
[2]Added as whole livers, 23.7% dry matter, 17.5% crude protein, 4.0% total lipids.
[3]40% lard; 25% fish oil; 20% linseed oil; and 15% safflower oil.
[4]High solubility (80%), Sigma Chemical, St. Louis, MO.
[5]High viscosity, Sigma Chemical, St. Louis, MO.
[6]Provided the following in mg/kg of diet except as noted: vitamin A as all-*trans*-retinyl acetate, 18,000 IU; cholecalciferol, 2000 ICU; vitamin E (all-*rac*-α-tocopheryl acetate), 150 IU; menadione (as menadione sodium bisulfite), 25; thiamin (as thiamin mononitrate), 15; riboflavin, 15; vitamin B-6, 25; vitamin B-12, 0.042; nicotinic acid, 200; calcium pantothenate, 50; folic acid, 4.0; biotin, 1.0; choline Cl, 1500; inositol, 50; para-amino-benzoic acid, 50; ascorbic acid, 450; ethoxyquin, 150.
[7]Provided the following in mg/kg of diet: Mn (as MnO_2), 240; Zn (as ZnO), 200; Fe (as $FeSO_4 \cdot 7H_2O$), 120; Cu (as $CuSO_4$), 20; I, 4.2; and Ca, 300–360 (as $Ca(IO_3)_2$ and limestone).
[8]Provided 0.1 mg Se/kg of diet as sodium selenite.
[9]Based on analysis of ingredients.
[10]Does not include added carboxymethylcellulose; corn is assumed to be 71.2% carbohydrate by difference.
[11]By analysis.

TABLE 2

Effect of alligator treatment on alligator total length, gains in body weight, dry matter consumption and feed efficiency (experiment 1)

Dietary treatment				Weeks 1–15			Weeks 9–15
Fat	Corn	Protein	N	Final total length	Dry matter consumption	Body weight gain	Body weight gain
	%			*cm*	*g*	*g*	*g*
4.0	18.0	61.4	3	71.9	629	691	327
6.4	5.4	68.6	3	70.7	700	722	346
6.4	30.6	50.1	3	71.1	666	707	371
12.0	—	67.9	3	71.1	647	725	372
12.0	18.0	54.6	6	74.7	817	951	537
12.0	36.0	41.4	3	73.9	779	809	437
17.6	5.4	59.1	3	75.9	856	1004	522
17.6	30.6	40.6	3	72.6	804	872	511
20.0	18.0	47.8	3	76.4	888	991	538
Standard error				0.9	43	47	36
Regression analysis							
Parameter estimates							
Intercept				63.657	404.8	233.8	-13.916
Corn				0.4434	12.263	24.111	16.395
Fat				0.8587	34.2175	64.434	52.056
Corn × corn				-0.0078	-0.29275	-0.538	-0.3835
Corn × fat				-0.0126	-0.05925	-0.417	0.01287
Fat × fat				-0.0142	-0.77125	-1.567	-1.5035
Total regression							
p				0.001	0.001	0.001	0.001
R^2				0.629	0.600	0.712	0.688
Predicted optimum response							
Corn				6.3	18.8	15.2	18.6
Fat				27.4	21.5	18.5	16.5

times (Table 1, **Table 2**). Data were analyzed using the response surface regression procedures of SAS Institute (13). Response variables were body weight gain, final total length, dry matter consumption, feed efficiency, digestibility of protein and energy and DE. The initial design was established with corn and fat as independent dietary variables. In subsequent analyses, response variables were also evaluated in terms of digestible protein, carbohydrate and various components of dietary energy. Carbohydrate content of the diet was based on the carbohydrate content of corn, calculated as 71.2% by difference.

Experiments 2 and 3 were designed as a 2 × 4 factorial experiments with diet and feeding schedule as main effects. In both experiments, alligators were fed either a higher protein ("protein") diet or a lower protein diet in which corn or corn dextrin replaced protein sources (the "carbohydrate" diet) (Table 1). Treatment combinations were replicated four times. The factorial analysis was performed using the general linear model (GLM) procedure of SAS Institute (13). In the analysis of linear and quadratic trends in these data, additional observations (four replicates) of alligators that were concurrently fasted to promote weight loss were utilized. This facilitated regression analysis by broadening the range of feeding schedules, feed intake and weight changes. It also permitted estimation of daily protein and energy requirements for maintenance and maximum growth. Regression of mass-specific daily changes in body weight against mass-specific daily consumption of energy and protein yielded estimates of daily requirements for maintenance (y intercept = 0) and maximum growth, taken here to be represented by the peak of the quadratic curve fit to the data. Body weight was recorded only at the initiation and termination of these experiments, and the average of these two weights was used to calculate mass specificity of body weight gain and consumption.

RESULTS

Experiment 1. Final total length, body weight gain, dry matter consumption, and feed efficiency were significantly responsive to and predictable on the basis of

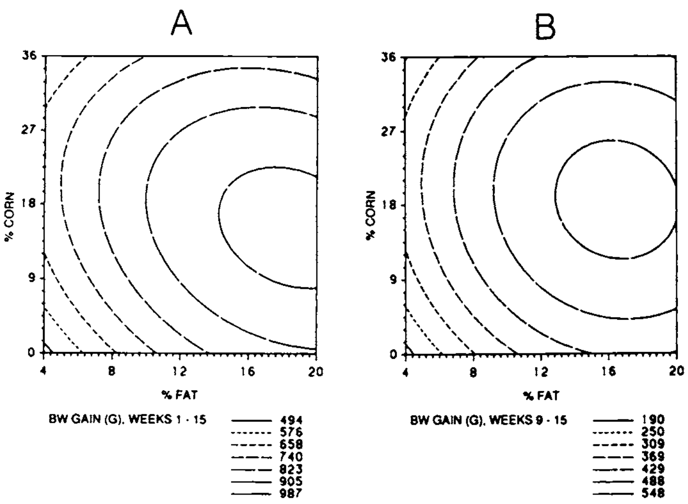

FIGURE 1 Response surface analyses of body weight (BW) gains from experiment 1, plotting (***A***) 15-wk gains and (***B***) gains during wk 9–15 as functions of the percentages of dietary corn and fat.

dietary corn and fat levels (Table 2). Coordinates for the predicted maxima for these response variables ranged from 6.3–18.8% corn and 15.8–27.4% fat.

Analysis of gains in body weight for the 15-wk study predicted a maximum response at 15.2% corn and 18.5% fat (**Fig. 1A**). The minimum response in weight gain was associated with diets in the low fat, corn-free portion of the response surface. The response to dietary corn depended on fat level of the diet. Increasing corn beyond 16–25% of diet, depending on dietary fat level, resulted in diminished weight gains. At high levels (20%) of dietary fat, diets with up to 27% corn supported body weight gains superior to or equal to those of alligators fed the corn-free diets. At lower and middle levels (4–12%) of dietary fat, corn content up to 36% of diet produced body weight gains equal to or greater than higher protein, corn-free diets of similar fat content. The body weight gain response surface generated from data for the last 7 wk of the experiment (Fig. 1*B*) indicated that for all levels of dietary fat, alligators fed diets with up to 36% corn performed the same as those fed higher protein, corn-free diets with the same level of fat. Furthermore, compared with results for the entire experiment, the predicted response surface maximum over the later weeks was slightly shifted toward greater levels (18.6%) of corn and lower levels (16.5%) of fat (Table 2; Fig. 1).

The modeled responses of final total length, dry matter consumption and feed efficiency (**Fig. 2**) were generally similar to those for body weight gain. Predicted diets for maximum responses always contained some corn and relatively high levels of fat. Compared with the results for body weight gain, the maximum response in final total length was predicted at lower levels of corn

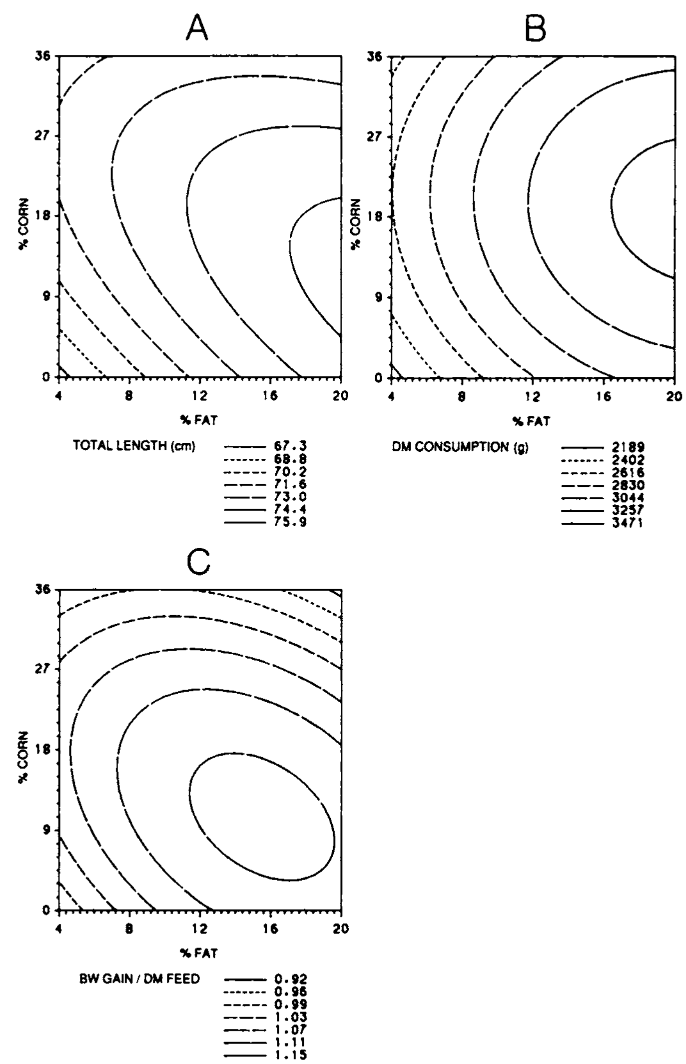

FIGURE 2 Response surface analysis of 15-wk data from experiment 1, plotting (***A***) final total length, (***B***) dry matter (DM) consumption and (***C***) feed efficiency [body weight (BW) gain:dry matter feed consumption] as functions of the percentages of dietary corn and fat.

(6.3%) and higher levels of fat (27.4%). Dry matter consumption was predicted to be maximum for dietary levels of 18.8% corn and 21.5% fat. Replacement of protein sources with corn, up to 36% of diet, resulted in improved consumption over corn-free diets with corresponding levels of dietary fat. However, feed efficiency was maximized at lower levels of corn (11.4%) and fat (15.8%) than was consumption. Furthermore, both feed efficiency and final total length were reduced by levels of dietary corn in excess of 20–25%.

Protein digestibility was significantly influenced by diet (**Table 3**). The presence of corn tended to decrease protein digestibility, but the reduction was slight, and protein digestibility was high for all diets. The decrease appears to be a function of carbohydrate content of the diet (**Fig. 3**). Generally (between 4 and 16% dietary fat

TABLE 3

Effect of dietary treatment on protein and energy digestibility and on digestible energy (DE) (experiment 1)

Dietary treatment						
Fat	Corn	Protein	Energy[1]	Protein digestibility	Energy digestibility	DE
	%		*kcal/kg*	%		*kcal/kg*
4.0	18.0	61.4	4734	87.7	85.3	4038
6.4	5.4	68.6	4982	87.7	85.0	4234
6.4	30.6	50.1	4669	85.6	84.2	3930
12.0	0	67.9	5283	87.7	85.0	4485
12.0	18.0	54.6	5051	86.9	83.9	4236
12.0	36.0	41.4	4824	85.8	83.9	4046
17.6	5.4	59.1	5331	87.3	83.7	4464
17.6	30.6	40.6	5085	85.9	84.7	4307
20.0	18.0	47.8	5266	85.9	83.0	4406
Standard error				0.6	0.7	37
Regression analysis						
Parameter estimates						
Intercept				88.7	—	4225
Corn				–0.06368	—	–19.9825
Fat				–0.03080	—	22.80295
Corn × corn				–0.00083	—	0.07402
Corn × fat				0.00272	—	0.54682
Fat × fat				–0.00317	—	–0.31919
Total regression						
p				0.017	0.363	0.001
R^2				0.419	0.193	0.908
Predicted optimum response						
Corn				< 0	—	< 0
Fat				< 0	—	36.6

[1]By analysis.

and 40 and 60% dietary crude protein), increases in the level of dietary fat led to slight increases in protein digestibility. Energy digestibility averaged 84.3 ± 0.7% and was not significantly influenced by either dietary corn or fat levels (Table 3). Digestible energy varied with and was highly predictable from dietary carbohydrate and fat levels because levels of these dietary variables generally reflected the range in dietary gross energy (**Fig. 4**). Analysis of the various production performance criteria in terms of digestible protein and energy (**Table 4**) indicated a digestible protein requirement between 42 and 49% of diet coupled with an energy requirement of between 42 and 49% of diet coupled with an energy requirement of 4374–4421 kcal/kg DE.

Experiments 2 and 3. The predominant treatment effect in experiments 2 and 3 was feeding schedule (**Table 5**). In both experiments, varying the number of feedings per week significantly influenced dry matter consumption and gains in body weight.

Although dry matter consumption was not significantly influenced by diet, animals fed carbohydrate-containing diets averaged greater gains in body weight

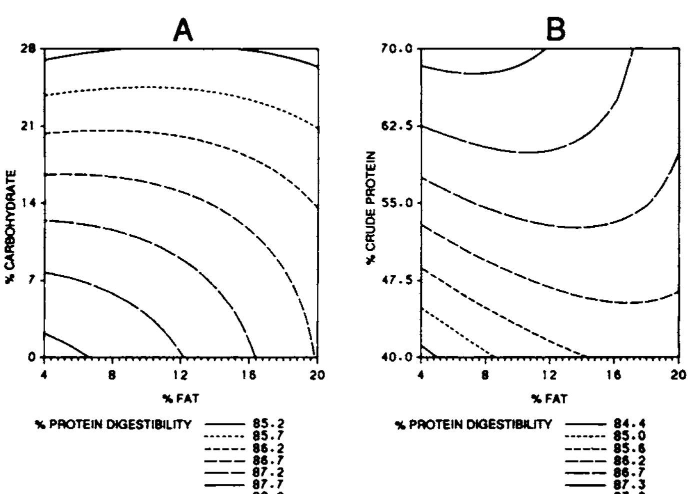

FIGURE 3 Response surface analysis of the protein digestibility data from experiment 1. Protein digestibility is plotted as a function of the percentages of dietary fat and (***A***) carbohydrate and (***B***) crude protein.

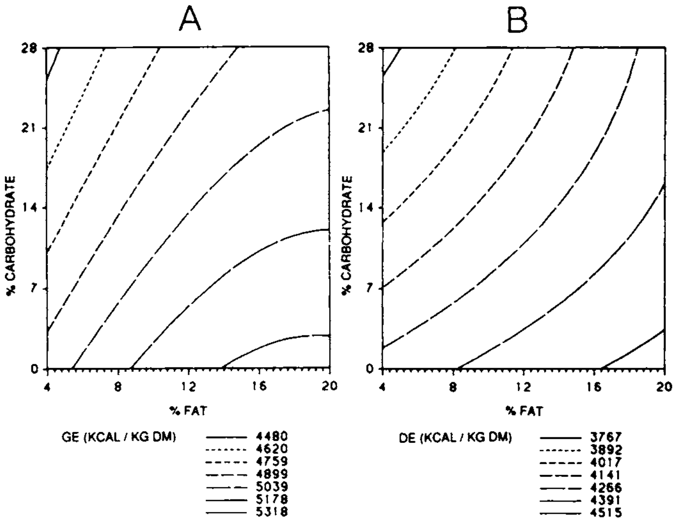

FIGURE 4 Response surface representation of dietary (***A***) gross energy (GE) and (***B***) digestible energy (DE) as functions of the percentages of dietary carbohydrate and fat. DM = dry matter.

(Table 5). This influence approached significance ($p < 0.08$) in experiment 2 and was highly significant in experiment 3 (mean = 550 g for the carbohydrate diet vs. 492 g for the carbohydrate-free diet). These greater body weight gains appear to be attributable to improved feed efficiency with the carbohydrate diet; the effect of diet on feed efficiency was significant in experiment 3.

Fasted animals lost an average of 32 g over 5 wk in experiment 2 and 61 g over 4 wk in experiment 3. Regression of body weight changes against the number of days fed per week (**Fig. 5**) indicates quadratic responses in both experiments. Maximum body weight gains were achieved with 5–6 d of feeding. Body weight could apparently be maintained with less than one feeding per week.

Regression analysis (**Fig. 6**) of results from experiment 2 indicated that the daily maintenance requirements for energy and protein were 5.7 kcal/kg body weight and 0.49 g/kg body weight, respectively. Regression of mass-specific daily body weight gain against protein intake indicated a maximum daily growth rate of 16.9 g/kg body weight. This growth rate and the required protein intake were achieved in experiment 2. However, the maximum growth rate predicted by regression of mass-specific daily body weight gain against energy consumption was not achieved (**Table 6**). Thus, for the energy intakes achieved, the protein requirement for maximum growth was met with either level of dietary protein.

Because diet was a significant source of variation in body weight gain in experiment 2, regression analysis of mass-specific growth was performed for each diet. Analysis of body weight gains supported by the protein diet in experiment 3 (**Fig. 7**) predicted daily energy and protein maintenance requirements of 8.4 kcal/kg body weight and 0.89 g protein/kg body weight, respectively. For the carbohydrate diet, the corresponding daily main-

TABLE 4

Regression analysis of total length, body weight gain, dry matter consumption and feed efficiency as functions of digestible protein (DP) and digestible energy (DE) (experiment 1)

Independent variable	Dependent variable: Final total length	Body weight gain	Dry matter consumption	Body weight gain/ dry matter consumption
	cm	*g*	*g*	*g/g*
Parameter estimates				
Intercept	−258.0604	−24,751.253	−17,105	−5.34272
DP	0.8145	40.5466	14.361	0.02813
DE	0.1440	11.3574	8.090	0.00264
DP × DP	−0.0198	−1.1404	−0.57384	−0.00060
DP × DE	0.0002	0.0143	0.007888	−0.000007
DE × DE	−0.00002	−0.0014	0.000964	-3.364×10^{-7}
Total regression				
p	0.001	0.001	0.001	0.042
R^2	0.589	0.651	0.567	0.367
Predicted optimum coordinates				
DP	45.1	45.1	42.5	48.7
DE	4382	4374	4367	4421

TABLE 5

Influence of feeding schedule and diet (carbohydrate vs. protein diets) on average dry matter consumption, body weight gain and feed efficiency for experiment 2 (5 wk) and experiment 3 (4 wk)

	Days fed per week	Dry matter consumption[1]		Body weight gain[1]		Feed efficiency[1,2]	
		Carbohydrate	Protein	Carbohydrate	Protein	Carbohydrate	Protein
		g				*g/g*	
Experiment 2	2	430	399	557	487	1.30	1.22
	3	504	499	610	570	1.23	1.14
	5	642	582	721	626	1.12	1.07
	6	702	722	817	880	1.16	1.22
Standard error		3.5		3.7		0.13	
ANOVA *p*							
Diet		0.289		0.080		0.386	
Days fed		0.001		0.001		0.027	
Diet × days fed		0.434		0.042		0.537	
Experiment 3	1	209	212	223	196	1.08	0.89
	3	556	519	653	578	1.18	1.11
	5	604	557	696	558	1.16	1.01
	7	619	641	627	637	1.01	0.99
Standard error		4.0		4.1		0.18	
ANOVA *p*							
Diet		0.529		0.023		0.030	
Days fed		0.001		0.001		0.060	
Diet × days fed		0.683		0.168		0.518	

[1]Analyzed as a 2 × 4 factorial experiment; values represent averages for replicates of two alligators each over the 5- and 4-wk periods, respectively.
[2]Body weight gain:dry matter consumption.

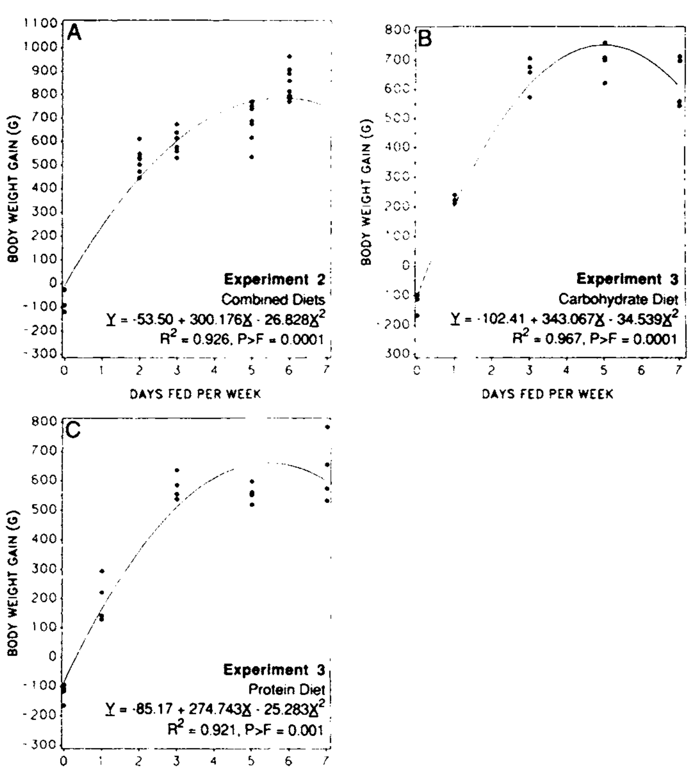

FIGURE 5 Body weight changes in experiments 2 and 3 plotted against the number of days fed per week. In experiment 2 (***A***), diet was not a significant source of variation and data are combined for the carbohydrate and protein diets. In experiment 3 (***B, C***) diet-related body weight gains were significantly different and are plotted separately.

tenance energy and protein requirements were 7.2 kcal/kg body weight and 0.68 g protein/kg body weight. Peak values for the regression equations were not within the range of mass-specific body weight gains observed in this experiment (Table 6). It appears that alligators did not consume amounts of protein or energy required for maximum growth in this experiment. However, from Table 5 and visual inspection of Figure 7, it can be seen that those animals fed the carbohydrate diet more closely approached both protein and energy requirements for maximum growth than those fed carbohydrate-free diets.

DISCUSSION

These experiments demonstrate that alligators can, within limitations, utilize and benefit from the presence

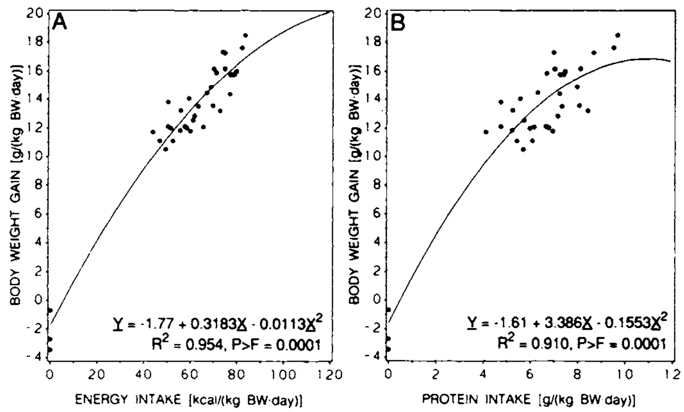

FIGURE 6 Regression of daily body weight changes per kilogram of body weight in experiment 2 as a function of daily mass-specific energy intake (***A***) and protein intake (***B***). Data for the carbohydrate and protein diet were regressed jointly because there were no diet-related significant differences in body weight gain.

of dietary carbohydrate and fat. In experiment 1, response surface analyses indicate that carbohydrate and fat would be included in diets formulated for maximum performance, by all production criteria. Minimum responses in production criteria generally occurred with low fat, carbohydrate-free diets. The fact that energy digestibility did not vary with diet indicates that the responses were not merely an indication of the net ability of alligators to digest and assimilate these dietary energy sources. Apparently, carbohydrate was digested about as well (roughly 85%) as other energy sources over the range of dietary variables in this study. Within the range of 0–20% corn (0–14% carbohydrate) and 4–12% fat, approximately twofold substitutions of carbohydrate for fat are predicted to result in equivalent body weight gains (Fig. 2). This ratio is approximately proportionate to that required to make the substitution isocaloric, as fat has roughly twice the caloric content of carbohydrate. At higher (> 15–20%) levels of dietary carbohydrate, responses to dietary carbohydrate become neutral, and eventually negative, with respect to the body weight gain response.

The maximal limits of carbohydrate utilization may be due to digestive or physiological phenomena. It is possible that the element of time, that is, the rate of digestion and assimilation, partially explains the decreased growth responses observed when dietary carbohydrate exceeds optimal levels. As true carnivores that lack plant carbohydrates in their natural diet, alligators may respond to dietary plant carbohydrates with a limited pancreatic output of amylytic enzymes, as has been reported for carnivorous fish (14, 15). More time for digestion would therefore be required. In alligators, digestive events generally take place over a number of days, rather than hours (1). An important consequence of a decreased rate of digestion would be to decrease the rate of food passage through the gastrointestinal tract. Ultimately, this would result in reduced food consumption and growth.

The physiological demand for glucose for maintenance and maximum growth in an ectothermic carnivore may be expected to be relatively low. There is no dietary energy demand for heat production to maintain elevated body temperatures. Furthermore, endogenous glucose and glycogen are normally derived from gluconeogenesis, an energetically inefficient process. Presumably, physiological levels of glucose and glycogen would be maintained at relatively low levels. Under

TABLE 6

Experiments 2 and 3: comparison of observed and predicted maximum mass-specific growth rates and the predicted protein and energy required for predicted maximum growth

		Mass-specific growth rate as a function of:								
		Days fed/week			Protein intake			Energy intake		
Experiment	Diet	5	6	7	Predicted maximum growth rate	Required protein consumption	Observed growth as a % of predicted maximum	Predicted maximum growth rate	Required energy consumption	Observed growth as a % of predicted maximum
		g/(kg BW·d)					%	*kcal/(kg BW·d)*		%
2	Combined	—	16.9 ± 1.0[1]	—	16.9	10.9	100	20.8	141	81.3
3	Carbohydrate	12.0 ± 0.6	—	11.1 ± 1.5	13.2	7.7	87.5[2]	13.2	82	87.5[2]
3	Protein	10.0 ± 0.5	—	11.2 ± 1.6	12.7	9.6	83.5[2]	13.0	93	81.5[2]

[1]Mean ± SD. Units are grams per kilograms of body weight (BW) per day.
[2]Combined results for five and seven feedings/wk.

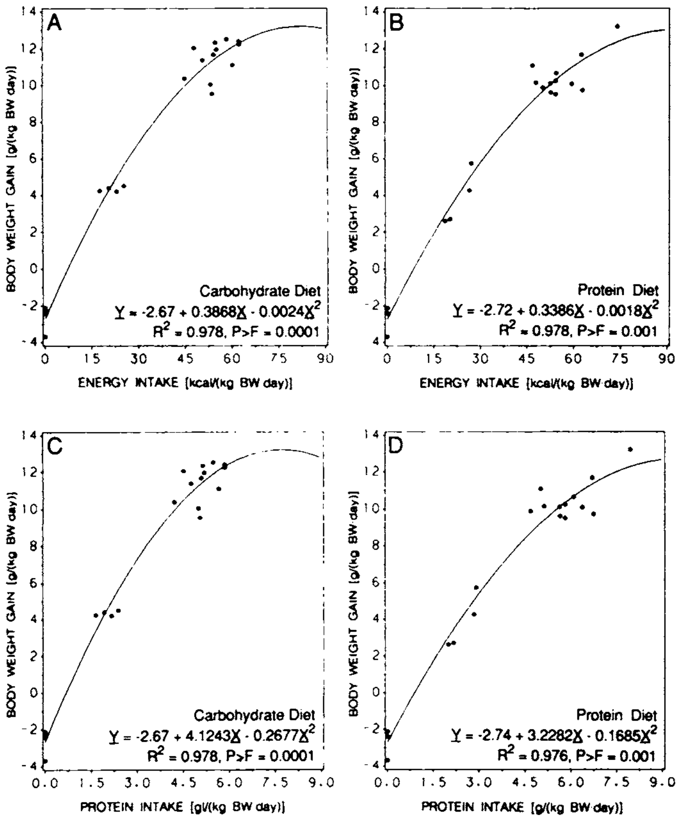

FIGURE 7 Regression of daily body weight changes per kilogram of body weight in experiment 3 as a function of daily mass-specific energy intake (***A, B***) and protein intake (***C, D***). Because diet was a significant source of variation in body weight gains, data for the carbohydrate (A, C) and protein (B, D) diets are plotted separately.

proper dietary conditions, it appears, for example, that 11% dietary carbohydrate (15% corn) can satisfy these limited requirements for glucose (Fig. 2) and thus spare use of protein as a gluconeogenic substrate. When dietary energy exceeds the demand for maintenance and growth, that is, during periods of fat deposition, carcass fat would be more efficiently derived from dietary fat than from carbohydrate because of the energetic costs of lipogenesis. It is of interest, therefore, that we have demonstrated elsewhere (3, 5) that the fatty acid composition of fat from the total carcass and from a variety of tissues closely resembles dietary fat.

It is possible that the relatively low upper limits of optimal dietary carbohydrate utilization by alligators may also be a function of a limited secretion of insulin in response to dietary carbohydrate. Carnivores, in general, are physiologically predisposed to gluconeogenesis for endogenous production of glucose (16). As an apparent consequence, carnivorous fish display a limited insulin response to dietary glucose (17–19). Hilton and Atkinson (20) noted a growth depression in rainbow trout fed glucose at 21% of diet. Staton et al. (3) reported a growth depression in young alligators fed glucose at 20% of dietary dry matter, as compared to growth supported by a carbohydrate-free purified diet.

At low levels of dietary fat, the projected 3.0% decrease in protein digestibility (Fig. 3) over the range of dietary carbohydrate fed in this study is numerically similar to the 3.2% dietary protein contributed by corn included at 36% of diet. The view of Coulson and Hernandez (1) that vegetable proteins are not digestible by alligators could be used to explain this observed decrease in protein digestibility associated with increased dietary corn. However, this rationale alone is likely to be incorrect. Recently, we (3) demonstrated that another vegetable protein, isolated soybean protein, was well-digested by alligators when making up more than 40% of dietary protein. Furthermore, Coulson et al. (21) report several plant proteins to have been partially digested. Increasing dietary fat had the effect of increasing protein digestibility at lower levels of dietary crude protein (Fig. 4). Coulson et al. (21) indicated that dietary fat slowed the rate of digestion of dietary protein. This slowing process could be associated with the slowing of food through the gut, which would increase the opportunity for digestion and absorption.

In experiment 1 (Table 4), maximal responses in growth (weight and length) were predicted at digestible energy (DE) and protein (DP) levels that result in a calculated DE:DP (kcal/g protein) ratio of 9.7:1. Using the average protein digestibility coefficient of 86.7%, an optimal DE:crude protein ratio of 8.4:1 can be calculated. From experiment 2 the predicted maximum daily requirements for gross energy (GE) and crude protein (CP) can be used to calculate a required GE:CP ratio of 12.9:1. From experiment 2, the predicted maximum daily requirements for GE and CP can be used to calculate a required GE:CP ratio of 12.9:1. From experiment 3, the optimum ratio is estimated as 10.6:1 with the carbohydrate diet and 9.7:1 with the carbohydrate-free diet. Using average energy digestibility coefficients to calculate DE:CP, optimum ratios would be 10.9, 8.9 and 8.2:1, respectively. These values are in relatively close agreement to the optimum DE:CP ratios (7.8–9.7:1) reported for warmwater fish species (11) during the growth phase.

From the data obtained in these experiments, it would appear that feeds for young alligators should contain 45% digestible protein, a caloric density between 8.2 and 10.9 kcal of DE per gram of CP, and a total of 11% readily digestible carbohydrate. To achieve this, added fat would be essential. Assuming 86.7% protein digestibility, the feed would have to be a minimum of 51.9% crude protein. Amino acid composition could alter this requirement.

Our findings that feeding alligators 7 d/wk is counterproductive was not unexpected. Current recommendations to alligator farmers are to feed only 5 d/wk for the first year of life, and three times weekly until the animal reaches harvest or breeding size (22).

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