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DIET COMPOSITION AND BLOOD VALUES OF CAPTIVE CHEETAHS (*ACINONYX JUBATUS*) FED EITHER SUPPLEMENTED MEAT OR COMMERCIAL FOOD PREPARATIONS

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Abstract: Nutrition most certainly affects health and may play a role in the etiology of growth and reproductive problems in captive cheetah (*Acinonyx jubatus*) populations. The objective of our research was to examine nutritional differences between two dietary regimens and quantify their physiologic effects on cheetahs held in captivity. Twelve cheetahs were randomly assigned to either a commercial diet (COM) or a supplemented meat diet (SMD) group. These cats were physically examined and had blood samples taken three times over the course of a year. Representative samples of COM and four separate components of the SMD treatment were analyzed over the same time frame for proximate nutrient composition, digestibility, and concentrations of taurine, fat-soluble vitamins, and selected minerals. Concentrations of fat, vitamins A and E, Se, Fe, Cu, Na, and Mn were significantly higher in COM compared with those in SMD samples, with the exception of fat content in turkey. Mg content was lower in COM than in SMD; other nutrients did not differ. Mean concentrations of vitamins A and E in COM were markedly higher than in SMD samples (408,140 vs. 29,696 IU/kg dry matter [DM] and 431 vs. 48 IU/kg DM, respectively) and varied dramatically between sampling periods. Percent crude protein and protein-to-fat ratios were high for SMD compared with either whole prey–based or commercial food preparations. Blood urea nitrogen and serum creatinine levels were above normal reference means for domestic cats. Plasma concentrations of vitamins A, D, and E were significantly higher in COM-fed than in SMD-fed cheetahs. Both plasma retinol and tocopherol levels were almost three times higher in COM-fed cats (1.26 ± 0.06 vs. 0.53 ± 0.03 μg/ml and 17.5 ± 0.7 vs. 6.4 ± 0.02 μg/ml, respectively) and exceeded the normal ranges expected for domestic felids. Significant differences between male and female cheetahs were found for plasma concentrations of vitamin E, Se, and Fe after allowing for effects of diet and time of collection. Excess fat-soluble dietary vitamins can result in direct toxicities as well as nutrient antagonisms and may be linked to reproductive and health issues in captive cheetahs. The high protein levels found in SMD may be linked to chronic renal disease, which was detected in some of these cheetahs.

Key words: Cheetah, *Acinonyx jubatus*, nutrition, diet, captivity.

INTRODUCTION

Genetic bottlenecks in cheetahs (*Acinonyx jubatus*) have been cited as the source of low fecundity, high infant mortality, and reduced growth rates.[44] However, carnivores in general exhibit significantly lower levels of genetic variation than do other mammals;[42] thus, other factors are likely to contribute to these problems. Management conditions,[29] behavior,[9,10] and dietary factors[16,26,53] have been cited as potential underlying causes of low rates of reproductive success in North American captive cheetah populations.

Although domestic cats appear to be a suitable physiologic model for cheetahs and other felids,[16] nutritional deficiencies still account for 7% of the mortality in captivity for cheetahs <6 mo of age.[40] Health problems in adult cheetahs, such as reproductive abnormalities[53] and dental pathologies,[9] may be linked to dietary factors. Fatty acid imbalances[12] can also result in health problems, and hepatic disease has been linked to vitamin A toxicosis.[26]

In nature, cheetahs consume a wide variety of vertebrate prey[47] that is likely to vary in nutrient composition seasonally. In contrast, captive cheetahs are often fed commercially prepared diets with little variation in texture and composition, and this may contribute to some of the health issues seen.[16] Many facilities supplement commercial diets (COMs) with meat obtained opportunistically (e.g., carcasses) in an effort to duplicate the natural variability of cheetah diets as well as to work within

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economic constraints. A third management strategy for captive felids involves feeding solely supplemented meat or whole carcasses.[63]

Whereas psychologic effects of feeding these various diets have been investigated,[9] the objectives of our research were to: 1) examine compositional differences between the COM and the supplemented meat diet (SMD), 2) document potential physiologic differences in nutritional status between cheetah groups fed these two diet treatments, and 3) compare these values with parameters established for domestic cats.

MATERIALS AND METHODS

Study design

Twelve cheetahs at Wildlife Safari in Winston, Oregon, were randomly assigned to either COM (Nebraska Brand Canine Diet, Central Nebraska Packing, Inc., North Platte, Nebraska 69101, USA) or SMD (skeletal meat) groups, after blocking for sex (n = 6 per group). Commercial canine rather than feline formulations are typically used in feeding programs for captive cheetahs because of their lower overall fat content and the fact that other nutrient concentrations meet the nutritional recommendations established for cats.[16] All animals had previously been maintained on SMD, were occasionally supplemented with COM, and were fed 1.14 kg of diet once daily.

Supplemental meat diets comprised skeletal muscle (cattle, horse, deer, or turkey drumstick) sprinkled with 1.5 g vitamin supplement (Chaparral® Zoological Vitamins, Chaparral Sales Corp., Albuquerque, New Mexico 87101, USA) and 1.5 g $CaCO_3$ (laboratory grade). Label specifications for Chaparral Zoological Vitamins include the following (dry matter [DM] basis): vitamin A (578.7 IU/g), vitamin D_3 (385.8 IU/g), vitamin E (570.3 mg/kg), folacin (13,230 mg/kg), niacin (1,160 mg/kg), pantothenic acid (137 mg/kg), riboflavin (179 mg/kg), thiamin (68.3 mg/kg), vitamin B_{12} (2,200 μg/g), vitamin B_6 (35.3 mg/kg), Ca (0.71%), Cu (75 mg/kg), I (0.01 mg/kg), Fe (1,430 mg/kg), Mg (0.01%), P (0.72%), K (0.02%), and Zn (19.8 mg/kg). A single meat was offered randomly on a daily basis. Over the course of a year, the following proportions were fed: beef and horsemeat (each 35% approximate wet weight), deer (20%), and turkey (10%). There was no distinct seasonal pattern. Turkey drumsticks were offered intact (bone and skin) to cheetahs, whereas no bones or hides were included with ungulate meats. All meats were evenly coated with powdered supplements and were consumed completely.

Sample collection and analyses: diets

Three representative samples each of COM and four types of SMD were collected at 4-mo intervals for a total of three sampling periods over the course of a year (May, September, and January, 1997–1998). During one of the collection periods, only two samples of deer were submitted for analysis. The SMD samples were taken from prepared diets (including supplements), stored in plastic Zip-Lock® bags, and frozen at −20°C until analyzed to determine proximate composition, taurine, vitamins A, D_3, and E, and Ca, P, Fe, Na, K, Co, Cr, Cu, Mg, Mn, Mo, Se, and Zn mineral concentrations. For digestibility estimates, an additional 453 g of each diet was mixed with 2.2 g of chromic oxide (Cr_2O_3) before freezing and subsequent analysis.

Digestibility estimates were made for each collection period using Cr_2O_3 as an indigestible marker. Cr_2O_3 was incorporated into 1.14 kg of each diet at a rate of 0.57% wt/wt in the first trial. Subsequent trials incorporated a reduced Cr_2O_3 concentration of 0.35% wt/wt. All diets were fed for approximately 4 days before collection of fecal samples, and the cheetahs were watched to ensure that all of the diet was eaten and that no sharing occurred. At least 25 g of feces was collected from each cat and stored at −20°C in plastic bags until time of analysis. Feces were dried at 60°C, and representative samples were analyzed to determine concentrations of Cr_2O_3 according to standard spectrophotometric procedures.[23] Apparent DM digestibility was calculated according to previously published equations.[65]

In preparation for proximate analyses, thawed samples were passed three times through a meat grinder containing a 3-mm plate. Ground samples were subsequently analyzed in duplicate for percent moisture, crude fat, Kjeldahl nitrogen, and ash according to the Association of Analytical Communities methodology for meats.[3] For taurine analyses, 25-g diet samples were homogenized in nine volumes of water, and then 1 ml of 60 g/L sulfosalicyclic acid was added to 1 ml of the homogenate. This mixture was centrifuged at 10,000 g for 15 min at 4°C, and the supernatant was analyzed for taurine using an amino acid analyzer as described subsequently for blood and plasma samples. Trace mineral concentrations were determined on freeze-dried samples by inductively coupled plasma atomic emission spectroscopy (ICP-AES)[58] and atomic absorption spectroscopy (for Se).

Fat-soluble vitamin A and E concentrations were determined using methods[61] with published modifications.[6] Vitamin A activity was calculated as 0.3

μg retinol = 1 IU;[45] vitamin E activity was calculated as 1 mg α-tocopherol = 1.49 IU, 1 mg γ-tocopherol = 0.15 IU, and 1 mg δ-tocopherol = 0.05 IU.[31] For vitamin D_3 determinations, 5 g of diet was mixed with 5,000 counts per minute of ^{3}H-vitamin D_3 in 50 ml of ethanol, equilibrated at room temperature for 30 min, and then saponified in ethanol–KOH solution at room temperature.[3] After saponification, the samples were extracted with *n*-hexane, washed with distilled water repeatedly until all KOH was removed, and then passed through an anhydrous sodium sulfate column to remove residual water. The extracts were dried under a stream of nitrogen gas, redissolved in methanol, and applied to a C-18 cartridge as previously described.[11] The fraction containing vitamin D was sequentially purified by two normal-phase high-performance liquid chromatography (HPLC) runs, followed by one reverse-phase HPLC using 10% methanol in acetonitrile at a flow rate of 0.8 ml/min as the mobile phase to separate vitamin D_2 from vitamin D_3.

Sample collection and analyses: cheetahs

Blood samples were first collected 2 mo after the cheetahs started consuming the dietary treatments and again at 4-mo intervals when the diets were sampled. Physical examinations, parasite fecals, serum chemistries, and complete blood counts (CBC) were made at the time of each blood collection. Gastric endoscopies were performed during the first and last sampling periods to check for evidence of gastric ulceration. Photographs of each cheetah's oral cavity were taken to document dental condition immediately after cleaning at the start of the study and again 12 mo later at the end of the study.

Blood samples were collected from the saphenous vein from anesthetized cheetahs and divided into seven 1-ml aliquots for subsequent analyses using 1) heparinized and nonheparinized tubes for plasma and whole blood taurine analyses, 2) blue, heparinized tubes for vitamin and mineral analyses, 3) red-top tubes for serum chemistry and ceruloplasmin activity determinations, and 4) EDTA tubes for CBC evaluations. Whole blood, serum, or plasma samples collected to determine concentrations of taurine, vitamins, minerals, and ceruloplasmin activity were stored at −20°C until the time of analysis. Samples collected for vitamin analyses were wrapped in aluminum foil before freezing to prevent losses.

Plasma tocopherols and retinol were measured using HPLC techniques following modified methods.[57] A Series 400 liquid chromatograph (Perkin–Elmer, Inc., Norwalk, Connecticut 06850, USA) equipped with a 15-cm C18 reverse-phase column was used for separation. A fluorescence detector (PE Model LS-1) monitored α-, γ-, and δ-tocopherol concentrations. Retinol was assessed at 325 nm using a PE Model LC-95 spectrophotometer, and peak areas were analyzed against standards (Hoffmann–LaRoche, Inc., Nutley, New Jersey 07110, USA). Plasma vitamin D isomers (25-hydroxy-cholecalciferol and 1,25-dihydroxy-cholecalciferol) were quantified by radioimmunoassay using ^{3}H-25-OH-D_3 (Amersham TRK 396 Amersham, 800 Centennial Avenue, Piscataway, New Jersey 08855, USA or New England Nuclear NET-349 New England Nuclear, 549-3 Albany Street, Boston, Massachusetts 02118, USA) after sample extraction and silica Sep-Pak cartridge chromatography to eliminate other vitamin D metabolites.[11]

Plasma micro- and macromineral concentrations (Ca, P, Fe, Na, K, Cu, Mg, and Zn) were determined by using ICP-AES;[58] Se was assayed by atomic absorption spectroscopy. A complete digest was done to determine total P and Fe concentrations. Serum ceruloplasmin activity was determined,[50] and absorbencies were used to calculate activity using the following formula: $(A_{15} - A_5) \times 0.625$. For taurine analysis, whole blood was thawed and refrozen twice and then diluted onefold with distilled water to release all taurine from cells. To a portion of plasma and whole blood preparations, an equal volume of 60 g/L sulfosalicylic acid was added, and then the mixture was centrifuged at 10,000 *g* for 15 min at 4°C. Supernatants were analyzed to determine taurine concentrations using an amino acid analyzer (Beckman Model 121 MH, Beckman Instruments, Fullerton, California 92831, USA).

Statistics

Means and standard errors for dietary vitamins A, D_3, and E, taurine, and mineral concentrations and composition were calculated by averaging values for each of the four SMD components and COM over the three sampling periods. Individual SMD results (e.g., for horse, cattle, deer, and turkey) were pooled for comparisons between treatment groups. To determine the significance of differences for specific parameters between SMD and COM, and among SMD components, individual *t*-tests and various multiple pairwise comparisons were performed, respectively. Seasonal variations in SMD composition and element concentrations are described (e.g., May, spring; September, fall; January, winter), but because this study was conducted for only 1 yr, there was no way to statistically evaluate apparent differences between these time periods.

Table 1. Nutrient concentrations in commercial (COM) and four supplemented meat[a] diets (SMDs) fed to cheetahs (*Acinonyx jubatus*) in captivity (mean ± SE).[b]

Nutrient	Commercial[c] (n = 9)	Horse (n = 9)	Cattle (n = 9)	Turkey (n = 9)	Deer (n = 8)
Composition (%)					
Dry matter	33.4 ± 0.5	28.5 ± 1.1	25.4 ± 9.0[d]	30.9 ± 1.0	27.8 ± 0.9[e]
Moisture	66.6 ± 0.5	71.5 ± 1.1	74.6 ± 26.4[d]	68.9 ± 1.0	72.2 ± 0.9[e]
Crude protein	59.0 ± 0.5	77.8 ± 3.3	83.8 ± 29.6[d]	68.4 ± 2.7	82.6 ± 3.6[e]
Crude fat	23.02 ± 0.99	12.19 ± 2.71	9.14 ± 3.32[d]	24.73 ± 2.55	9.84 ± 2.94[e]
Ash	8.04 ± 0.35	5.36 ± 0.30	5.92 ± 2.09[d]	4.99 ± 0.25	5.75 ± 0.58[e]
DM digestibility (%)	75.7	76.7	76.7	76.7	76.7
Minerals (mg/kg)					
Ca	15989 ± 1344	7697 ± 1190	13634 ± 4545	15472 ± 3205	16651 ± 6618
P[f]	11066 ± 781	6071 ± 521	6984 ± 2328	6814 ± 656	8516 ± 542
Fe[f]	452 ± 24	191 ± 35	214 ± 71	220 ± 51	249 ± 59
Na[f]	3456 ± 147	1035 ± 89	1502 ± 501	2114 ± 122	1478 ± 127
K	6956 ± 189	9919 ± 834	10306 ± 3435	7906 ± 430	10975 ± 382
Se	0.61 ± 0.03	0.18 ± 0.04	0.14 ± 0.05	0.68 ± 0.04	0.09 ± 0.02
Co	<0.10	<0.10	<0.10	0.33 ± 0.02	<0.10
Cu[f]	9.1 ± 0.3	3.4 ± 0.5	3.1 ± 1.0	4.5 ± 0.7	5.6 ± 0.0
Mg[g]	714 ± 41	956 ± 72	1135 ± 378	1170 ± 119	1406 ± 229
Mn[f]	25.8 ± 1.6	8.4 ± 1.8	11.0 ± 3.7	11.9 ± 2.4	12.8 ± 3.2
Mo	<0.30	<0.30	<0.30	<0.30	<0.30
Zn	115.6 ± 2.9	68.4 ± 7.5	130.5 ± 44.0	97.5 ± 3.2	81.6 ± 11.2
Cr	0.4 ± 0.1	0.6 ± 0	1.3 ± 0.4	1.2 ± 0.6	0.9 ± 0.1
Concentration					
Vitamin A (IU/kg)[f]	408140 ± 5520	40465 ± 29909	17892 ± 5964	30444 ± 17725	30020 ± 25191
Vitamin E (IU/kg)[f]	431 ± 72	40 ± 9	63 ± 21	8 ± 1	89 ± 13
Vitamin D_3 (ng/g)[h]	51	13	39	53	6
Taurine (g/kg)[i]	1.8 (1.76–1.84)	1.4 (0.28–2.81)	1.2 (0.24–2.46)	6.6 (4.33–10.40)	3.8 (2.81–5.29)

[a] SMDs consisted of 1.14 kg skeletal muscle sprinkled with 1.5 g vitamin supplement (Chaparral® Zoological Vitamins, Chaparral Sales Corp., Albuquerque, New Mexico 87101, USA) and 1.5 g laboratory-grade $CaCO_3$.

[b] All values except moisture and dry matter (DM) expressed on a DM basis.

[c] Nebraska Canine Diet, Central Nebraska Packing, Inc., North Platte, Nebraska 69101, USA.

[d] $n = 8$.

[e] $n = 6$.

[f] $P < 0.001$; two-way analysis of variance (ANOVA) between COM and SMD treatments.

[g] $P = 0.002$; one-way ANOVA on ranks between COM and SMD treatments.

[h] Concentrations of vitamin D_3 represent single analyses of diets prepared by homogenizing samples collected in May, September, and January.

[i] Mean (range) concentrations of taurine based on $n = 3$.

Means and standard errors for plasma vitamins A, D, and E, taurine, and mineral concentrations and serum ceruloplasmin activity were calculated on the basis of collection period (May, September, and January), gender, and diet treatment. Initial graphs illustrated potential differences between diets, sampling period, and gender. Two-way repeated-measures analysis of variance (ANOVA) was used to test for significant differences between blood measures for COM and SMD, sampling period, and potential interactions. Missing data points were handled by using a general linear model (Type III or adjusted sums of squares). A three-way ANOVA tested for significant effects of gender after accounting for sampling period and diet. Because these cheetahs were not randomly selected from a larger population, inferences are limited to this group of animals.

RESULTS

Diets

Although the SMD treatment group received a variety of meats, results for each type of meat are presented individually but were compared statistically with the COM treatment group as a pooled data set (Table 1). Fat, vitamins A and E, Se, Fe, Cu, Na, P, and Mn concentrations were all signifi-

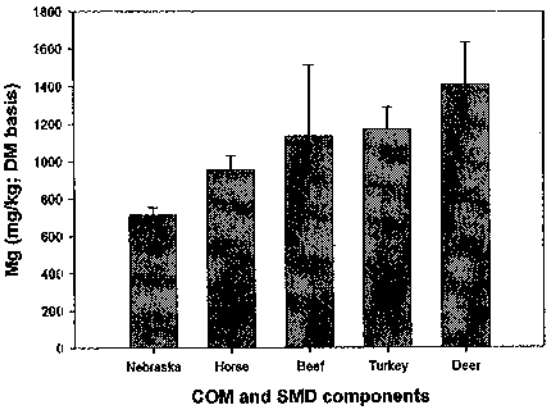
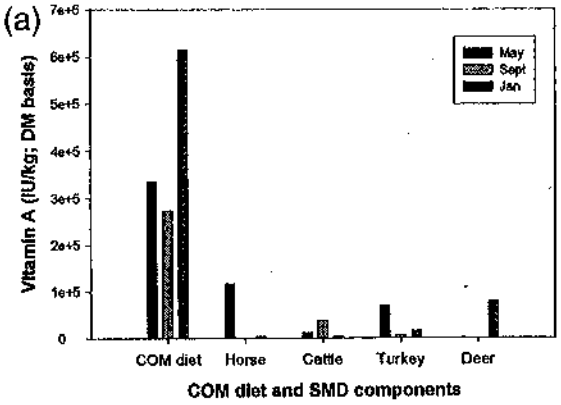


Figure 1. Variations in Mg concentrations between COM diet and SMD components ($P = 0.002$; one-way ANOVA on ranks between COM and SMD treatments).

cantly higher in COM as compared with SMD ($P < 0.001$). However, turkey was similar to COM in fat content and Se concentration. Only concentrations of Mg were lower in COM (714 ± 41.3 vs. 1,160 ± 75.31 mg/kg DM; $P = 0.002$; Fig. 1). Mean concentrations of Fe were generally higher in COM (452 mg/kg) than in SMD (218 mg/kg; $P < 0.001$; Table 1), and this difference was most apparent between COM and horse, cattle, and turkey meats. Similarly, Mn and Cu concentrations were higher in COM than in each SMD component. Sodium concentration was significantly higher in COM than in SMD ($P < 0.001$).

The commercial and turkey diets were relatively high in fat content, approximately 24% of DM compared with an average of 10% for the other SMD components (Table 1). The mean concentration of vitamin A in COM was very high in comparison with that in SMD (408,140 ± 55,201 vs. 29,696 ± 11,285 IU/kg DM) and varied dramatically between sampling periods (Fig. 2a). Similarly, the concentration of vitamin E in COM was quite high (431 ± 72 IU/kg DM) in comparison with that in SMD (48 ± 6.9 IU/kg DM) and also varied dramatically between sampling periods (Fig. 2b). Among SMD components, turkey had significantly lower concentrations of vitamin E (8 ± 1 IU/kg DM) than did either cattle (63 ± 21 IU/kg DM) or deer (89 ± 13 IU/kg DM) ($P < 0.05$; Dunn's multiple pairwise comparison). However, concentrations of Se were highest in COM and turkey (0.61 and 0.68 mg/kg DM, respectively) compared with a mean range of 0.09–0.18 mg/kg for the other SMD components. The difference in means between horse and turkey components for Se was 0.497 mg/kg DM ($P < 0.0001$; t-test).



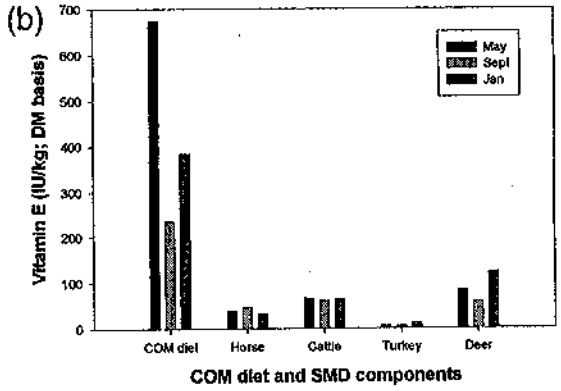


Figure 2. Fat-soluble vitamin A (**a**) and E (**b**) concentrations among dietary components and sampling periods ($P < 0.001$; two-way ANOVA between COM and SMD treatments).

Taurine concentration was highest in turkey and lowest in cattle (Table 1). One sample of each of the cattle and horse had an unusually low concentration of taurine (20% of the mean of the three samples). COM had the most consistent concentrations of this nutrient.

There were significant differences among sampling periods for SMD component concentrations of Ca and P, especially for Ca concentrations in deer, which were highest in September. In September, Ca concentrations for all SMD components averaged 19,513 ± 3,551.5 mg/kg DM (equivalent to 1.95%) compared with 7,727 ± 868.2 mg/kg DM (0.77%) in January. Again, samples were only collected for 1 yr, and so the significance of this finding is not known. Among SMD components, deer had the highest concentrations of Ca and P, whereas horse had the lowest. In general, horse tended to

Table 2. Hematologic and serum biochemical values for captive cheetahs (*Acinonyx jubatus*).[a]

Determination	Units	May 1997 (n = 12)	Jan 1998 (n = 10)	Reference values[21]
Hematologic				
Hematocrit (PCV)	%	38.84 ± 2.79 (29.3–58.7)	40.36 ± 1.17 (34.7–47.1)	30–45
Hemoglobin	g/dl	13.13 ± 0.93 (10.2–19.5)	11.81 ± 0.39 (10.5–14.5)	8–15
Red blood cell	$10^6/\mu l$	7.18 ± 0.42 (5.7–10.3)	6.88 ± 0.25 (6.0–8.3)	5–10
MCV[b]	fl	53.90 ± 1.35 (46.1–58.1)	58.82 ± 0.84 (53.3–62.4)	39–55
MCHC[c]	g/dl	33.82 ± 0.21 (32.8–34.8)	29.25 ± 0.33 (27.8–30.8)	30–36
MCH[d]	pg	18.22 ± 0.44 (15.9–20.0)	17.2 ± 0.27 (15.3–18.2)	13–17
White blood cell	$10^3/\mu l$	11.11 ± 0.92 (7.6–16.2)	10.99 ± 1.07 (6.9–17.6)	5.5–19.5
Neutrophils	$10^3/\mu l$	8.50 ± 0.78 (5.4–12.9)	7.71 ± 1.01 (4.9–15.7)	2.5–12.5
Lymphocytes	$10^3/\mu l$	1.99 ± 0.22 (0.9–3.1)	2.20 ± 0.20 (1.4–3.1)	1.5–7
Monocytes	$10^3/\mu l$	0.31 ± 0.06 (0.07–0.64)	0.10 ± 0.05 (0.1–0.5)	0–0.85
Eosinophil	$10^3/\mu l$	0.29 ± 0.09 (0.09–0.81)	0.96 ± 0.26 (0.18–2.8)	0–0.75
Biochemical				
Glucose	mg/dl	113 ± 3.96 (96–140)	122.1 ± 1.73 (112–128)	60.8–124.2
Cholesterol	mg/dl	176.6 ± 15.1 (133–335)	191.9 ± 15.5 (123–311)	71.3–161.2
Total protein[e]	g/dl	6.63 ± 0.14 (6.0–7.6)	6.6 ± 0.05 (6.1–7.2)	5.7–8.0
Albumin	g/dl	3.78 ± 0.08 (3.5–4.3)	4.33 ± 0.35 (3.6–7.4)	2.4–3.7
Uric acid	mg/dl	0.22 ± 0.004 (0.01–0.07)		
BUN[f]	**mg/dl**	**35.6 ± 3.0 (14.6–52.1)**	**41.0 ± 3.32 (28.0–65.0)**	**15.4–31.2**
Creatinine	**mg/dl**	**3.10 ± 0.18 (2.0–4.4)**	**2.64 ± 0.18 (1.9–3.9)**	**0.5–1.9**
Triglyceride	mg/dl	0.47 ± 0.08 (0.21–0.99)		
Total bilirubin	mg/dl	0.33 ± 0.03 (0.2–0.6)	0.14 ± 0.02 (0.1–0.2)	0.1–0.5
Globulin	g/dl	2.85 ± 0.08 (2.4–3.3)		2.4–4.7
GGT[g]	IU/L	6.67 ± 0.19 (6.0–8.0)		1.8–12.0
LDH[h]	IU/L	207.4 ± 39.3 (106–578)		35.1–224.9
AST[i]	IU/L	57.4 ± 6.9 (25–97)		9.2–39.5
ALP[j]	IU/L	25.8 ± 1.1 (22–30)	7.78 ± 0.54 (6–12)	12.0–65.1
ALT[k]	IU/L	124.6 ± 10.2 (66–198)	69.9 ± 4.06 (49–88)	8.3–52.5

[a] Values listed as mean ± SE (range).
[b] MCV = mean corpuscular volume.
[c] MCHC = mean corpuscular hemoglobin (Hb) concentration.
[d] MCH = mean corpuscular Hb.
[e] Refractometer.
[f] BUN = blood urea nitrogen.
[g] GGT = gamma glutamyltransferase.
[h] LDH = lactate dehydrogenase.
[i] AST = aspartate aminotransferase.
[j] ALP = alkaline phosphatase.
[k] ALT = alanine aminotransferase.

have comparatively lower concentrations of trace minerals among all SMD components (Table 1).

Cheetahs

A male and female cheetah in the SMD group were euthanized in August 1997 at 8 and 9 yr of age because of chronic renal failure, and so only four collections were taken from this group in September and January. Physical examinations during each collection period revealed no unusual findings; however, blood urea nitrogen (BUN) and creatinine levels were above the normal reference ranges for domestic cats (Table 2). The range for BUN in our cheetahs was 14.6–65.0 mg/dl, and creatinine levels ranged between 1.9 and 4.4 mg/dl (vs. reference ranges of 15.4–31.2 and 0.5–1.9 mg/dl, respectively, for domestic cats).[25] Up to 7 mo before euthanasia, these two cheetahs did show signs of weight loss and intermittent vomiting, but these clinical signs were originally attributed to gastritis. Gastric endoscopies provided gross evidence of mild-to-moderate ulceration in all the cheetahs in both diet groups. Histologically, lesions were described as mild-to-severe, chronic lymphoplasmacytic gastritis with intralesional spiral bacteria (presumably *Helicobacter* sp.). Dental tartar varied from mild to se-

Table 3. Plasma vitamin, taurine, and mineral concentrations in cheetahs (*Acinonyx jubatus*) fed two dietary treatments for 1 yr in captivity.

Component	Commercial diet[a] $\bar{x} \pm$ SE (n = 18)	Range	Supplemented meat diet $\bar{x} \pm$ SE (n = 14)	Range	Felid reference ranges
Concentration (μg/ml)					
Retinol[b]	1.26 ± 0.06	0.89–1.89	0.53 ± 0.03	0.40–0.94	0.2–0.6[16]
α-tocopherol[b]	17.5 ± 0.7	9.7–29.2	6.4 ± 0.2	2.7–10.5	5.99–8.02[16]
Vitamin D (ng/ml)[c]	17.0 ± 1.2	3.3–29.3	12.2 ± 0.6	6.0–22.1	
Taurine (nmol/ml)	154 ± 26	57–460	133 ± 16	45–271	60–120[d]
Taurine (whole blood; nmol/ml)	544.6 ± 48.81	332–832	562.1 ± 53.43	392–800	300–600[d]
Minerals (μg/ml)					
Ca	104.4 ± 1.1	97–119	104.5 ± 1.5	79–116	79–109[25]
P	72.8 ± 3.0	48–132	65.6 ± 2.2	47–178	40–73[25]
Na	3583 ± 19	3420–3890	3509 ± 30	2840–3710	
K	193.8 ± 6.2	160–300	177.9 ± 6.7	97–239	
Fe	1.22 ± 0.13	0.63–2.98	0.55 ± 0.02	0–0.61	12.2–38.5[35] (mmol/L)
Se (ng/ml)	471 ± 5	390–592	446 ± 22	250–534	
Cu	0.99 ± 0.01	0.74–1.55	0.74 ± 0.05	0.16–1.38	0.4–1.2[19]
Ceruloplasmin (U/L)[e]	20.5 ± 0.8	10.0–35.6	13.6 ± 0.9	1.9–25.6	
Mg	23.2 ± 0.4	19.5–28.6	24.2 ± 0.7	19.7–30.5	18–24[35]
Zn[f]	0.69 ± 0.02	0.50–0.90	0.92 ± 0.14	0.55–2.43	1.0–1.4[22]

[a] Nebraska Canine Diet, Central Nebraska Packing, Inc., North Platte, Nebraska 69101, USA.
[b] $P < 0.001$; two-way repeated-measures analysis of variance (ANOVA).
[c] $P < 0.005$; two-way repeated-measures ANOVA.
[d] See www.vetmed.ucdavis.edu/vmb/aal/nal.html.
[e] Serum concentrations.
[f] $P < 0.05$; two-way repeated-measures ANOVA.

vere, with no apparent correlation with diet treatment.

Plasma concentrations of α-tocopherol and retinol were significantly higher in COM-fed than in SMD-fed cheetahs ($P < 0.0001$; Table 3), as were vitamin D concentrations ($P = 0.005$). Mean plasma α-tocopherol concentrations in the COM-fed group were almost three times higher than in the SMD-fed group (17.5 vs. 6.4 μg/ml), mean retinol concentrations were over twice as high (1.26 vs. 0.53 μg/ml), and vitamin D concentrations averaged 17.0 ng/ml in COM-fed versus 12.2 ng/ml in SMD-fed cheetahs. Plasma concentrations of Fe and Cu also tended to be higher in COM-fed than in SMD-fed cheetahs, although the differences were not significant. Only concentrations of Zn were significantly lower in COM-fed cheetahs (0.69 vs. 0.92 μg/ml; $P < 0.05$).

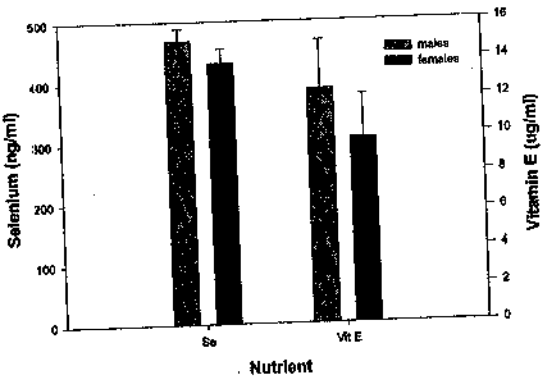


Figure 3. Differences in serum concentrations of Se and vitamin E between male and female cheetahs (*P = 0.044; three-way ANOVA).

Concentrations of α-tocopherol differed significantly between male (12.4 ± 2.58 μg/ml) and female (9.8 ± 2.27 μg/ml) cheetahs (Fig. 3) after allowing for the effects of diet and sampling period ($P = 0.044$). Plasma concentrations of Se also tended to be higher in male than in female cheetahs (472.8 ± 20.62 vs. 428.6 ± 21.18 ng/ml), whereas females typically had higher concentrations of Fe (1.32 ± 0.27 vs. 0.66 ± 0.14 μg/ml). Plasma Se concentrations of SMD-fed cheetahs were lower in May than in September ($P < 0.05$; Tukey pairwise multiple comparison); however, samples would need to be collected over a longer period of time to determine significance.

DISCUSSION

Whereas unsupplemented muscle meat clearly provides a nutritionally imbalanced sole diet for carnivores, appropriately supplemented chunk meat forms the basis of many successful captive feeding programs globally.[9,63] Feeding SMDs has the potential to improve appetites, enhance psychologic well-being, and perhaps minimize dental disease,[9,21] but SMDs still may provide suboptimal nutrition when evaluated chemically or physiologically (or both). Variability may mimic the reality of a natural predator–prey cycle, but direct comparative data are scarce. Nutrient differences among various SMDs can be significant, and a single supplement may not be suitable across meat types. Similarly, inappropriately formulated commercial preparations containing imbalances, excesses, and/or deficiencies of specific nutrients may affect health. This underscores the essentiality of routine dietary analyses and nutritional assessment as a foundation for captive species management.

The COM fed throughout this study was highly fortified and provided one-and-a-half to fivefold higher levels of most nutrients compared with recommendations established for felids. Vitamin A concentrations were considered excessive in COM; implications will be discussed in detail. SMD components, on the other hand, were highly variable in nutrient content. Individually fed, the supplemented horsemeat may have proven deficient in vitamin E as well as several minerals (Ca, P, Cu, Mn). Supplemented beef in this study was marginal in P and low in Cu and vitamin E, whereas deer was seasonally marginal in Se, but all other nutrient levels were considered adequate. Supplemented turkey meat fed to cheetahs (following protocols of this study) would provide a low-P, high-Se, marginal-Cu, and very low–vitamin E diet. Taken together, the mixed SMD treatment (calculated proportionately) should be considered low in vitamin E (50 ± 12 mg/kg DM) as well as in Cu (3.6 ± 0.6 mg/kg DM).

Average percent DM digestibility did not vary among dietary components in this study; these values were slightly lower than those of another COM (76% vs. 79%) fed to other large felids.[65] Lack of a significant difference in tooth and gum health between dietary treatments likely reflects individual genetic variation rather than a dietary causal factor per se. In order to minimize confounding treatments, none of the cheetahs were fed hard bones (as recommended for optimal oral health in large felids[9,63]) during the year of this study.

Of the SMD components examined, all would individually meet the minimum dietary protein (28% DM basis) and fat (9% of DM) levels recommended for felids. Only turkey (with skin), however, approximated the ratio of protein to fat displayed by COM (2:1). In comparison, the SMD components (excluding turkey) had a 6.6:1 protein-to-fat ratio, yet whole prey ratios are only 3:1.[17] Because both fat and protein digestion are used to meet the energetic needs of cats, with fat being preferentially metabolized, the high levels of dietary protein in the SMD diets may have contributed to the chronic renal disease (CRD) noted. Restricted protein diets (up to 28–30% DM) are generally recommended for cats diagnosed with CRD.[2] Commercial moist canine pet foods range in protein from 11.5% (prescription diets) to 41.7% DM, and similar feline diets range from 29.4% to 51.5% DM.[2] By comparison, the crude protein level for COM diet in our study was 59.0 ± 0.5% DM and ranged between 68.4 ± 2.7% and 83.8 ± 29.6% DM for SMD components. These high dietary protein levels might have contributed to the high serum BUN and creatinine levels found in all the cheetahs, irrespective of treatment. Decreased protein intake can limit progression of renal dysfunction in cats by reducing glomerular and interstitial lesions in kidneys[1] and by controlling serum creatinine concentrations.[28] Signs of uremia are also mitigated. The goal of dietary management is to achieve nitrogen balance so that endogenous proteins are not degraded. A negative nitrogen balance leads to protein deficiency, which is associated with anemia, hypoalbuminemia, loss of muscle mass, and dry, unthrifty coat.[2] Dietary lipid intake can also affect renal function (e.g., vasodilation) through changes in fatty acid metabolism (see discussion below). Other dietary nutrients of concern for cats with CRD include Na (not to exceed 0.35% DM), P (not to exceed 0.04–0.60% DM), energy, K, and Cl.[2]

Taurine is an essential amino acid in cats, required for the prevention of central retinal degeneration,[27] myocardial disease,[48] and other abnormalities.[59] Although problems with taurine deficiency have not been reported in cheetahs, they have been noted in other zoo felids, particularly those fed canned diets. The requirement for domestic cats ranges from 800 to 1,200 mg/kg DM for commercial, dry diets to as high as 2,500 mg/kg DM for processed, canned diets.[30] The higher requirement may be attributed to the lower digestibility of protein in canned diets,[4] resulting in bacterial overgrowth in the small intestine and subsequent bacterial destruction of taurine during the enterohepatic circulation of taurocholic acid. Alternatively, higher fat levels in such diets may increase enterohepatic

circulation of bile salt, and the subsequent deconjugation of such salts by intestinal bacteria would result in higher fecal excretion of taurine.[37] It is not known whether the cheetah makes taurine as many animals do or whether it is a dietary essential. All diets analyzed contained more than adequate levels of taurine. Furthermore, plasma and whole blood taurine concentrations found in the cheetahs, independent of diet, were above the range known to be adequate for the domestic cat and reported in free-ranging cheetahs.[16] Thus, both feeding regimens appeared adequate in providing this nutrient, and turkey may be a particularly good source. It is not possible to draw conclusions from this work as to whether taurine is an essential nutrient for the cheetah.

Percentage fat was considerably less in SMD components, with the exception of turkey, and more closely approximated the dietary recommendations for domestic felids. Turkey drumsticks were fed whole with the skin left on, accounting for the high percentage of fat (25%); however, cats purportedly handle high-fat diets well.[39] Felidae are obligate carnivores and exhibit fatty acid desaturase enzyme deficiencies, specifically Δ-6-desaturase.[7,15] Without this enzyme, animals are unable to convert linoleic acid to γ-linolenic acid, which is further converted to arachidonic acid by elongase and Δ-5-desaturase enzymes. Therefore, cats (including cheetahs[12,14]) have a dietary requirement for these longer-chain, more unsaturated fatty acids for numerous roles including maintenance of cell membranes, prostaglandin production, cell–cell interactions, and other functions.

We did not analyze diets for fatty acid composition, nor did we observe signs of essential fatty acid deficiencies documented in cheetahs, including impaired growth, dry skin, hair loss, skin lesions, and amenorrhoea.[12] Nonetheless, it is possible that deterioration of fatty acids occurs during storage and preparation of SMDs[14] to a higher degree than would be found in COMs. SMD ingredient collection, processing, and time to final distribution can take approximately 3 hr to several days, during which time fatty acid breakdown could happen. This is not a process to which cheetahs are regularly exposed in nature; wild cheetahs are considered to be pure hunters[8,49], and reports of scavenging are isolated.[47,54] The potential for oxidative deterioration of dietary fatty acids also suggests an increased requirement for dietary antioxidants, which would commonly be added to commercially prepared diets. To ensure that essential fatty acids are included in adequate quantities in captivity, especially during periods of higher physiologic need (growth, reproduction, and lactation),[13,56] meat diets can be additionally supplemented with plant oil–fish oil mixtures (3:1) at 2 ml/kg diet.[15] Detailed investigations are necessary to determine the need for such supplements with the current dietary treatments.

The fat-soluble vitamins A and E were markedly higher in concentration in COM than in SMD and resulted in plasma concentrations two to three times that of SMD-fed cheetahs. Increased dietary vitamin A concentrations parallel increases in the severity of hepatic lesions in cheetahs and may play a role in development of veno-occlusive disease.[26] Hypervitaminosis A in domestic cats has also been associated with reproductive disorders and skeletal abnormalities.[52] Additionally, high dietary vitamin A has been shown to antagonize the uptake and metabolism of vitamin E. Given the health problems linked to excess dietary vitamin A in captive cheetahs, concentrations measured in COMs should be of concern and should be corrected by the manufacturer. The supplementation product used in the SMD preparation appeared to have adequate concentrations of vitamins A and D but was low in vitamin E.

Variation among sampling periods in vitamin A and E concentrations in dietary components (Fig. 2a, b) may be partly attributable to some oxidative losses during handling. Oxidation or rancidification of dietary fats leads to reduced vitamin E content in the diet because of the role of vitamin E as an oxygen free-radical scavenger. Turkey and horsemeat, containing higher levels of polyunsaturated fats, are more prone to oxidation compared with meat from ruminant prey species (in this case, beef and deer). These samples also displayed the lowest vitamin E levels in our study, whereas preservatives and antioxidants in COM may have maintained higher vitamin E levels in that treatment.

Plasma concentrations of retinol and α-tocopherol (as measures of vitamins A and E, respectively) in SMD-fed cheetahs were similar to values given for cheetahs in previous studies.[18,51] Circulating fat-soluble vitamin concentrations are dependent on age, sex, and seasonal and dietary influences;[18] activity level, stress, disease, malnutrition, and estrogenic compound toxicity can also alter retinol metabolism.[20] Despite numerous variables contributing to fluctuations in plasma concentrations of α-tocopherol and retinol, these measurements can be used as indicators of dietary uptake and values were within normal ranges of body stores. Many carnivores have the physiologic flexibility for storage of excess vitamin A as nontoxic esters[51] (perhaps in response to prey compositional fluctuations

that vary seasonally), and short-term high retinol concentrations may in fact be quite normal. Nonetheless, chronic dietary excesses of vitamin A may contribute to liver and kidney stress as well as general health and reproductive issues reported in captive cheetahs. The very high level of vitamin E found in COM may offset the potential toxic effects of the excess vitamin A measured in this study. Additionally, the high levels of protein found in both diet treatments may inactivate plasma vitamin A through binding to retinol-binding protein. Concentrations of dietary vitamins A and E that are magnitudes lower in SMD than in COM resulted in normal physiologic ranges in the cheetahs studied.

Fat-soluble vitamins should be considered as a group when evaluating dietary adequacy because they work synergistically and in some cases antagonistically, particularly if imbalanced. Hence, dietary ratios of vitamins A:D:E are another issue of importance. Evidence suggests that dogs and cats are not able to synthesize vitamin D_3 adequately in the skin, thus making this vitamin a dietary essential.[32,33,43] Turkey and COM contained higher concentrations of vitamin D_3 compared with other SMD components (51–53 vs. 6–39 ng/g DM), coinciding with the higher percentage fat found in these two ingredients. The high vitamin A and E levels in COM do not appear to affect vitamin D uptake or measurement as a circulating metabolite in the cheetahs, at least over a 1-yr period. Although skeletal abnormalities, rickets, and metabolic bone disease have been reported in large felid species fed unsupplemented meat diets, no specific cases have been published on this subject in cheetahs, and the SMD treatment considered in this study appears adequate for vitamin D.

COM diets were less variable and, in general, contained higher levels of all mineral nutrients compared with SMD components. With the exception of Se and Zn, deer meat contained comparatively higher concentrations of all minerals than did the other meats analyzed, with horsemeat displaying the lowest mineral concentrations. Some authors report lower levels of most minerals in horsemeat,[5,38] whereas others[63] have found higher mineral concentrations in horsemeat than in cattle, deer, and turkey meats. Hence, it appears prudent, as a first step, to analyze raw ingredients of SMD for nutritional value on a routine basis and compensate for detected deficiencies or imbalances with proper supplementation.

Despite the wide differences in the mineral content of COM compared with that of SMD in our study, only plasma Zn concentrations differed significantly in cheetahs consuming these treatments. Because homeostatic mechanisms can delay or minimize diet-induced mineral concentration changes,[46,60] point-in-time analyses may not accurately represent an animal's mineral status and may preclude detection of abnormalities. Or, conversely, two- to fivefold differences in dietary mineral concentrations may be within normal ranges of dietary variability and should not be of concern as long as minimum dietary requirements are met and known antagonisms and interactions are kept within balance.

Copper concentrations were lower in all SMD components than in the COM diet, and plasma concentrations of Cu in cheetahs (both actual values as well as ceruloplasmin activity [a copper-containing enzyme]) reflected this finding but were within normal ranges listed for felids. In a previous study,[16] 81 captive cheetahs fed primarily COM had higher plasma concentrations of Cu and Zn (3.0 and 2.6 μg/ml, respectively), whereas Fe concentrations (0.88 μg/ml) were similar to those reported here. Interestingly, Cu and Zn are highly bound to protein and can be lost with severe proteinuria associated with CRD.[2] Plasma concentrations of Zn in COM-fed cheetahs were below the recommended felid range, whereas average concentrations for cheetahs in the SMD group were also low but closer to the reference range values. Copper deficiency has been repeatedly reported anecdotally in cheetahs[16] and can result in cub ataxia and hind-limb paralysis. Details of Cu requirements or metabolism are unknown; however, recent studies of Cu metabolism in the domestic cat have shown plasma concentrations of both ceruloplasmin and copper to be poor indicators of status.[22] Nonetheless, plasma concentrations of Cu, Zn, and Ca in cheetahs have been significantly correlated with sperm quality (Dierenfeld and Howard, unpubl. data). Therefore, mineral status of cheetahs may be linked to fertility, as it is in other cats.[34]

Assuming that normal cheetah plasma mineral concentrations fall within the range given for domestic felids, blood mineral concentrations still may vary according to gender,[55] nutritional intake, environmental factors (e.g., sunlight, season), interactions between other minerals and dietary components, and physiologic state.[24,36,41,60,62,64] There was some evidence of differences based on gender among some of the mineral concentrations. Female cheetahs tended to have twice the plasma concentration of Fe as did males, and higher levels of vitamin E and Se were found in males, irrespective of diet. If there is a difference in body fat deposition between male and female cheetahs, with females having a higher level of fat accumulation, it

may lead to increased demands for oxidative defense mechanisms in females and thus to lower concentrations of the antioxidants vitamin E and Se. Additionally, higher levels of circulating Fe may also lead to a higher oxidative load in female cheetahs. Further research needs to be conducted to explore any potential physiologic basis for such differences between males and females.

In conclusion, COM fed to captive cheetahs contained excessive levels of vitamins A and E compared with SMD, as detected by chemical analysis of diets as well as from circulating plasma concentrations in animals, and these levels should be adjusted to better meet known nutritional requirements of felids. Individual meats in the SMD treatment differed considerably in chemical composition, necessitating regular analysis of diets. Whole prey diets, as compared with skeletal meat diets, might be effective in reducing the unacceptably high ratio of protein to fat found in SMD components. The supplement used with the SMD treatment in this trial did not provide enough vitamin E, Cu, and possibly Se to meet minimum felid requirements; however, the plasma levels of these nutrients were adequate. The physiologic significance of differences between male and female cheetahs for plasma concentrations of vitamin E, Se, and Fe should be further investigated.

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