Do Maintenance Energy Requirements of Felids Reflect their Feeding Strategies?

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Maintenance energy (ME)requirements have been determined for the domestic cat, *Felis silvestris catus,* but not for larger felids. To determine if the domestic cat represents an appropriate model for studies with larger species, we measured digestive efficiency and digestible energy intakes in cats of different body sizes (body mass range: 15-195 kg)which included clouded leopard, *Neofelis nebulosa* (n = 9), cheetah, *Acinonyxjubatus* n = 6), Sumatran tiger, *Panthera tigris sumatrae* (n =4), lion, *Panthera leo* (n = 4)and Bengal/Siberian tiger, *Panthera tigris tigris/Panthera tigris altaica* (n = 2). Measurements were repeated seasonally. We found marked variation in crude protein (CP) and fat concentrations on a dry matter basis both among (44.9-57.7% CP; 22.2- 32% fat, n = 10) and within (48.7-59.1 % CP; 22.9-34.8% fat, n = 28) lots of one of the two commercial diets fed to cats. The apparent digestibility of dry matter, crude protein and energy of one frozen, meat- based diet did not differ among species or seasons. A second diet fed to some clouded leopards was less digestible. The ME intakes of tigers and cheetahs were considerably higher than was predicted based on that of the domestic cat, and when compared to those of lions and clouded leopards. The ME requirement of clouded leopards may be influenced by age. We hypothesize that the inter-specific differences reflect variation in metabolic rates and in energy expenditures which may be a consequence of different feeding strategies and predatory behaviors.

Key words: Felidae, maintenance energy requirements, digestible energy, dietary management

INTRODUCTION

The evolution of obligate carnivory involves a set of unique nutritional and metabolic requirements. For example, the domestic cat, *Felis silvestris catus,* requires arachidonic acid, taurine, preformed vitamin A, and preformed niacin in its diet, is relatively inefficient at conserving nitrogen, and maintains high gluconeogenic enzyme activities (MacDonald, Rogers and Morris, 1984; Rogers and Morris, 1982). Zoo animal nutritionists commonly use this information in formulating diets for captive zoo cats, regardless of body size. The domestic cat, while relatively small, seems the most appropriate model since controlled studies with cats in zoos are rarely possible. With the advent of commercially prepared and nutritionally complete foods for cats, the incidence of nutritional pathologies associated with feeding unsupplemented muscle meat has disappeared in modern zoos.

While the quantitative nutrient requirements of the domestic cat provide useful guidelines in feeding exotic cats, the validity of metabolic size as a predictor of energy needs is not well established. Body size in felids ranges from under 2.5 kg to over 250 kg. McNab (1989) observed that body size, food habits, climate and activity level may all influence energy expenditure among species of the Carnivora, which have highly varied expenditures.

The energy expenditure of mammals is often predicted from body size using an equation based on the scaling of body weight to the 0.75 power ($BW_{kg}^{0.75}$) (Kleiber, 1975). However, since domestic cats are relatively uniform in size it is common to express energy requirements relative to body mass rather than metabolic body size. According to the "Nutrient Requirements of the Cat" (NRC, 1986) a 4 kg adult requires 280-320 kilocalories (kcal) of metabolizable energy daily or approximately 70 and 80 kcal per kg body weight for inactive and active cats, respectively. However, recent work with domestic cats, representing a range of body sizes, indicates that the relationship between digestible energy intake and body mass may not be so simple. Earle and Smith (1991) reported that the digestible energy intake of the adult cat at maintenance is about 71 and 43 kcal/kg BW in 2.5 kg and 6.5 kg cats, respectively.

We conducted four digestion trials in each of four seasons to assess energy, protein and dry matter digestibility. We examined the effect of season and of varying body size in cats, ranging in mass from 15 to 195 kg, on maintenance energy requirements and determined if requirements can be predicted based on metabolic body size.

METHODS

Twenty five felids, housed at the National Zoological Park, Washington, DC and at the Conservation and Research Center, National Zoological Park, Front Royal, Virginia were used in the trials. The cats represented five species/subspecies: clouded leopard, *Neofelis nebulosa* (n = 9) , cheetah, *Acinonyx jubatus* n = 6) , Sumatran tiger , *Panthera tigris sumatrae* (n = 4), lion, *Panthera leo* (n = 4) and Bengal/Siberian tiger , *Panthera tigris tigris/Panthera tigris altaica* (n = 2) .

Most cats had access to both indoor and outdoor enclosures during each 4-6 day digestion trial, with the exception of cheetahs. Cheetahs were maintained in outdoor enclosures but had access to heated shelters during inclement weather . Clouded leopards had unrestricted access to indoor and outdoor enclosures. Their building is cool in summer and heated to maintain at least 21 degrees C in the winter. Lions and tigers were maintained in both indoor (heated and cooled) and outdoor enclosures during digestion trials and spent approximately 50% of their days in each area. Ambient daily temperatures were recorded during each of the four digestion trials.

Cats were individually fed raw, horsemeat-based diets that have been shown to maintain body weight. Seven clouded leopards were fed Nebraska Brand Frozen Feline Diet (Animal Spectrum, North Platte, Nebraska, 69103) and two were fed Nebraska Brand Frozen Canine Diet (Animal Spectrum, North Platte Nebraska 69103). All other cats received Canine Diet. Food samples were taken during each trial and frozen for later analysis. Cats were weighed before and after each digestion trial. Chromic oxide was homogeneously mixed into the ration at a rate of 0.5% of dry matter. Fecal samples were collected daily and frozen. Lions, tigers and cheetahs were fed separately but otherwise were housed in pairs or groups. Feces voided by individual lions, tigers and cheetahs were distinguished by the presence of 15-20 grains (cracked corn, safflower, and millet) that had been mixed into the food before feeding. Upon thawing, feces from each cat were pooled for each trial, and grains and contaminating hair were manually removed. Food and feces were oven dried at 55 degrees C and ground in a Wiley mill to pass a 2 mm mesh screen. Subsamples of food and feces were assayed for crude protein by macro-Kjeldahl (TN X 6.25), fat by Soxhlet ether extraction, energy by Adiabatic bomb calorimetry and chromium by atomic absorption spectroscopy after perchloric and nitric acid digestion.

RESULTS

Analyses of ten lots of Canine Diet revealed marked variation in protein and fat. As percent of dry matter (DM) crude protein (CP) ranged from 44.9 to 57.5%, and fat ranged from 22.2 to 32.0%. Within a lot (sampled from 28 packages) variation in CP and fat was also high with a mean CP of 52.1% (CV = 5.6%)and a mean fat of 31.3% (CV = 10.4%). Variation in CP and fat in three lots of Feline Diet was not as great. Crude protein ranged from 38.0 to 41.2% and fat ranged from 36.1 to 40.3% on a DM basis.

Individual cats maintained body weight over the course of the one year study, indicating that they were being fed at a maintenance level. The mean weights for each species/subspecies at each trial period pre presented in Figure 1.

The apparent energy digestibility of the Canine Diet did not differ among species/subspecies (means of 93 to 94%) or among seasons; however the energy digestibility of the Feline Diet, fed to clouded leopards, was only about 90%.

Among clouded leopards, there was considerable variation among individuals in digestible energy intake (DEI), expressed relative to metabolic body size (MBS). It appeared that older cats had lower intakes (Figure 2). Such large individual differences were not seen in other species. The range in daily DEI expressed relative to MBS (kgo.75) in cheetahs was approximately 150 to 185; in lions, approximately 100 to 150; and in tigers, approximately 200 to 260. Among all cats there were no consistent seasonal patterns in energy intake.

Average digestible energy intakes (DEI) of individual cats are plotted against body mass in Figure 3. A large difference in energy intakes of lions and tigers was evident. For example, the DEI of large male lions was only about half that of the similarly sized male Bengal X Siberian tigers.

The natural logarithm (In) of digestible energy intake was plotted against In body mass to examine the scaling of energy intake to body mass (Figure 4). All cats did not appear to follow the same scaling relationship. For example, lions and young clouded leopards appeared to fall on the predicted line that represents extrapolation of the maintenance energy requirements of domestic cats, but cheetahs, Sumatran tigers and Bengal X Siberian tigers had considerably higher energy intakes.

DISCUSSION

These data clearly indicate that it is not possible to predict the maintenance energy needs of exotic cats from those of domestic cats. Moreover, the differences among species are not simply due to body size, but appear to reflect species-specific differences in metabolic strategies.

It is important to recall that these cats were all maintained in enclosures that did not permit high levels of activity; the differences in expenditure could be even greater among free-ranging cats. As we did not monitor behavior, we were unable to determine if differences in expenditure were paralleled by differences in activity level of the different cat species. Differences in resting metabolism may also be involved. McNab (1989) reported considerable variation among carnivores in metabolic rates, but did not directly compare the species of felids included in this study.

The particularly low energy intakes of old clouded leopards were remarkable. A reduction in the amount of food offered had been necessitated by the propensity to obesity in these cats; whether there is a corresponding reduction in activity level is not known .

The daily DE intakes relative to MBS in cats in this study compare to those reported for two adult leopards *(Panthera pardus)* by Barbiers, et al. (1982). The leopards (mean weight male, 53.8 kg; female, 41.1 kg) during the eight month study were found to have daily DE intakes of 182 and 166 kcal/kg 0.75, respectively. These were similar to those of the cheetah reported here (150 to 185 kcal/kg 0.7S).

In contrast to the divergent energetics of these various species/subspecies of cats, digestive ability did not appear to differ among species/subspecies, at least when a highly digestible, ground diet was fed. The digestibilities observed in this study were similar to previous reports on exotic cats fed raw, meat-based diets (Hackenburger and Atkinson, 1983; Barbiers, et al., 1982; Mills, 1980). Wynne (1989) reported much lower CP digestibilities in tigers and lions, although different prepared diets were used in that study.

We speculate that different species of cats have developed diverse metabolic strategies, and that these strategies involve considerable differences in maintenance energy requirements (Emmons, 1991). Some, such as clouded leopards and lions, appear to have relatively low energy expenditures that conserve energy by minimizing activity. Others, such as cheetahs and tigers, appear to expend considerably more energy, which is presumably related to foraging style. Although logistically difficult, the measurement of energy expenditures, via doubly labeled water, of various cat species under field conditions might help explain the differences reported here.

ACKNOWLEDGMENTS

This research was supported by a grant from the Waltham Centre for Pet Nutrition. The authors also thank the Friends of the National Zoo for support. The following animal care staff willingly shared their knowledge of cats and provided assistance during the animal trials: Stuart Wells, Lisa Wilson, Wayne Millner, Jeanne Minor and Ken Lang. Larry Collins permitted use of the clouded leopards. We thank Michael Jakubasz who provided technical and logistical support during laboratory analyses. Lindsey Scott, Kim Stewart, Sherry Holt and Lynn Sederlof assisted with sample processing.

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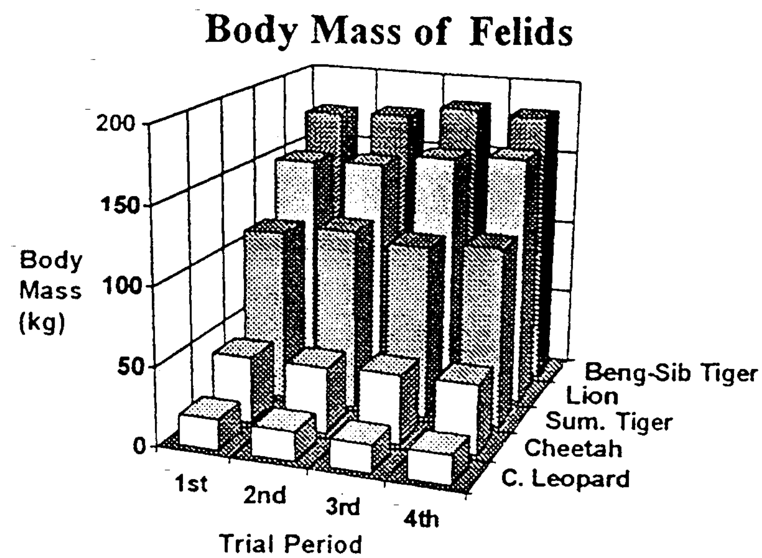

Figure 1. Body mass of clouded leopards, cheetahs, Sumatran tigers, lions and Bengal/Siberian tigers during each of four seasons. Mass measurements, in kilograms (kg), were taken before and after each digestion trial.

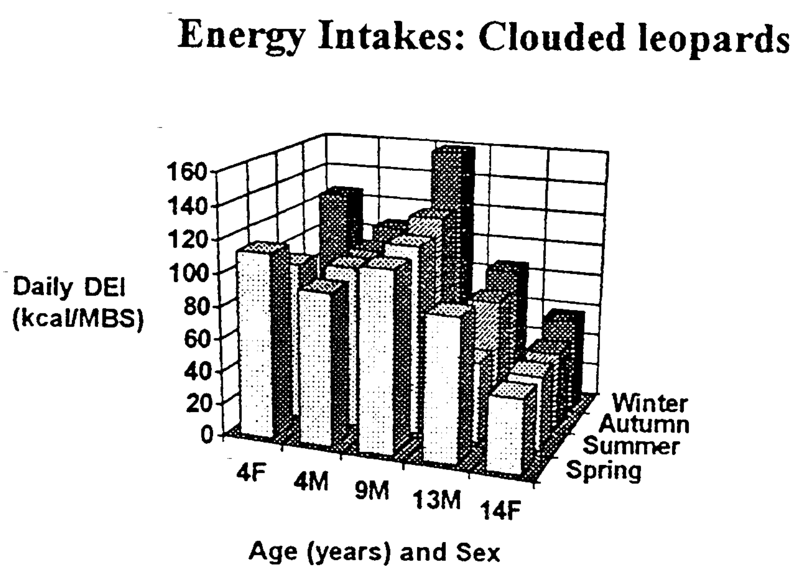

Figure 2. Digestible energy intakes (DEI) in kilocalories per metabolic body size (kcal/MBS) of clouded leopards during digestion trials conducted in each of four seasons. Differences in DEI by age and sex are shown. On X axis numbers represent age in years and letters indicate gender: M = male and F = Female.

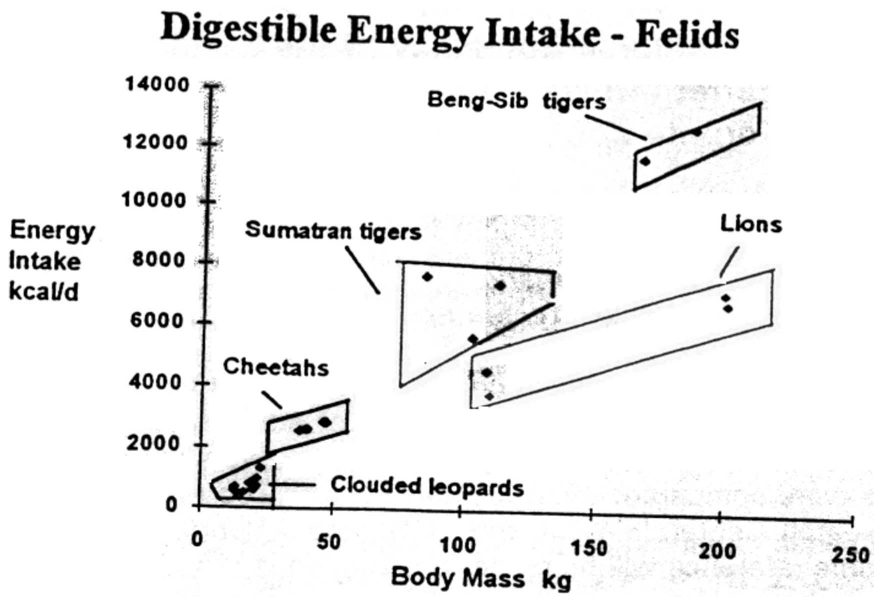

Figure 3. Digestibility energy intake of cats, in kilocalories per day kcal/day), plotted against body mass.

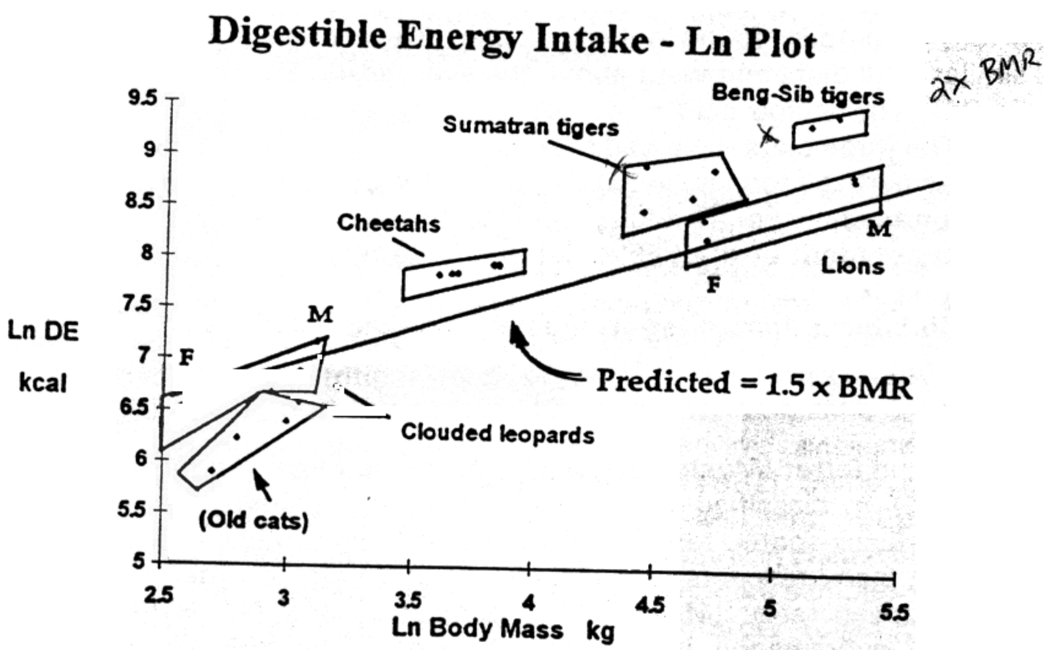

Figure 4. Natural logarithm (ln) of digestible energy (DE) intake in kilocalories (kcal) of cats plotted against the natural logarithm of body mass in kilograms (kg).