

Nutritional and Behavioral Effects of Gorge and Fast Feeding in Captive Lions

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Nonhuman animals in captivity manifest behaviors and physiological conditions that are not common in the wild. Lions in captivity face problems of obesity, inactivity, and stereotypy. To mediate common problems of captive lions, this study implemented a gorge and fast feeding schedule that better models naturalistic patterns: African lions (*Panthera leo*) gradually adapted from a conventional feeding program to a random gorge and fast feeding schedule. Digestibility increased significantly and food intake and metabolizable energy intake correspondingly decreased. Lions also showed an increase in appetitive active behaviors, no increase in agonistic behavior, and paced half as frequently on fast days as on feeding days. Thus, switching captive lions to a gorge and fast feeding schedule resulted in improved nutritional status and increased activity.

In the modern zoo, the well-being of nonhuman animals is an important consideration for housing, feeding, and management of the animals. To improve the well-being of captive animals—what Newberry (1995) called improvement in biological functioning—zoos endeavor to create enriched environments that elicit a wide range of natural behaviors. The zoos emphasize active, functional behaviors (Carlstead, Seidensticker, & Baldwin, 1991; Forthman, et al., 1992;

Maki, Alford, Bloomsmith, & Franklin, 1989; Shepherdson, 1994) and reductions of abnormal behaviors (Boccia, 1989; Carlstead et al., 1991; Odberg, 1987). Enrichment can focus on structural or physical changes to the environment such as size, cage furniture, complexity, and novelty (Carlstead, et al., 1991; Kleiman, 1994; Wechsler, 1992). In addition, changes to food availability can also be used to provide enrichment (Bond & Lindburg, 1990; Forthman et al., 1992; Law, 1993; Shepherdson, Carlstead, Mellen, & Seidensticker, 1993).

Captive carnivores, especially those who feed exclusively on vertebrates, pose unique challenges for creating enriched environments that will allow them to behave like their wild counterparts. Shepherdson et al. (1993) simulated more natural wild feeding patterns (and reduced pacing) in small cats by providing live prey and presenting multiple hidden and nonhidden daily feedings. Bond and Linburg (1990) found that feeding carcasses to cheetahs improved and prolonged feeding behaviors. However, feeding live prey or carcass feeding is not a common practice in North American zoos. The use of slaughtered livestock with large felids is discouraged (Bush et al., 1998) because of the potential harm from barbiturates used to euthanize feed animals. Whole animal carcasses of small animals is suggested as a substitute "upon occasion to vary the diet" (Shoemaker, n.d., p. 7). Thus, in the absence of carcass feeding, other characteristics of the natural feeding patterns of lions, such as meal size and frequency, may be manipulated to provide enrichment.

Often daily, or with one fast day per week, lions in captivity conventionally are fed a nonvarying diet of processed meat at regular, fixed, and frequent intervals (Meyer-Holzappel, 1968; Shoemaker, n.d.). In the hours preceding a scheduled feeding, lions in captivity often engage in pacing and repetitive stereotyped motor patterns (Carlstead & Seidensticker, 1991; Meyer-Holzappel, 1968; Shepherdson et al., 1993). In contrast, lions in the wild do not eat every day or on a fixed interval. Schaller (1972) reported that lions eat at an average rate of every 2.5 days in the plains and 3 to 3.5 days in the woodlands, although hunting success rates vary with season and habitat. Stander (1992) observed a more frequent rate of feeding (95 of 145 nights). However, this greater rate of feeding may be due to feeding his population smaller prey than that of other African lions (Stander, 1992; Stander & Albon, 1993; van Orsdol, 1984; Viljoen, 1993).

In addition, the conventional feeding regime for lions in zoos tends to promote obesity (Newberry, 1995; Schaller, 1972). Like wild lions, who sleep 20 to 21 hr a day (Schaller, 1972), captive lions are highly inactive. Wild lions burn calories in hunting and scavenging activities. With no opportunity to expend energy and burn calories, captive lions gain weight. Increasing the activity of these lions may help mediate the problem of obesity.

The purpose of this study was to provide enrichment to five captive lions by shifting them from a conventional zoo feeding schedule of predictable, fixed, small, daily (except Sundays) feedings to a more naturalistic gorge and fast schedule characterized by greater amounts of food offered less frequently and less pre-

dictably. We hypothesized that shifting the lions to a more natural pattern of feeding would reduce stereotypic pacing and elicit more activity. In addition, we hypothesized that a gorge and fast feeding schedule would affect digestion: Less frequent consumption of meals would increase overall diet digestibility because of improved efficiency of using nutrients. Finally, we predicted the combination of improved digestibility and increased activity would result in weight loss over time.

METHOD

Subjects

One male and four female captive African lions (*Panthera leo*) at the Topeka (Kansas) Zoo (Table 1) were housed as a pride in a 12 hectare, naturalistic, outdoor enclosure during the day and smaller, indoor quarters with access to a small (3.5 m × 6 m) outdoor pen at night. During medical checkups, the zoo veterinarian measured the lions' body weights. Measurements were taken from 2 months before the study began through 4 years after the study ended: The zoo maintained the lions on the gorge and fast feeding schedule for 2 years past the 10-week study period.

Feeding Schedule

During the course of the 10-week study, the lions slowly were adapted from a conventional schedule of once-daily feedings (except Sundays) to a more naturalistic gorge and fast feeding schedule of just three meals per week. One fast day was added to the schedule every 2 weeks. Lions were fed according to the conventional schedule during Weeks 1 and 2 and were fed 5 days per week in Weeks 3 and 4, 4 days per week in Weeks 5 and 6, and 3 days per week in Weeks 7 and 8. The lions were maintained on the 3-day-a-week feeding schedule during Weeks 9 and 10: These weeks were designated as the target weeks for measurement and comparison to the conventional feeding schedule. Fasting days each week were selected randomly, and no restrictions on the pattern of fasting days were imposed. Lions could and—on one occasion did—fast for 4 days in a row (eating on the evening of the fourth day). Lions fasted on Sunday on the conventional schedule of Weeks 1 and 2. Week 9, they fasted on Sunday, Tuesday, Friday, and Saturday. Week 10, they fasted on Monday, Wednesday, Thursday, and Friday. Throughout the study period, lions received bones twice a week—Wednesday and Sunday.

In the afternoons, lions were fed individually. Across weeks, total weekly food portions were held constant; the food amounts were divided equally across the number of feeding days each week. The females received 13.6 kg, and the male was of-

ferred 16.3 kg of food each week. During the conventional feeding schedule, the male was fed 2.7 kg and the females were fed 2.3 kg of food on each of the 6 feeding days. With the gorge and fast schedule, the male was offered 5.4 kg; the females were offered 4.5 kg of food on each of the 3 feeding days. The food that the lions were fed consisted of a frozen ground horsemeat-based mixture containing supplemental vitamins and minerals designed to be a complete and balanced diet for captive feline carnivores (Nebraska Brand Feline Food, Central Nebraska Packing, Inc., North Platte, Nebraska). Lions were given the opportunity to eat their meals until they walked away. Leftover food was removed, weighed, recorded, and discarded.

Observations

Across the 10 weeks of the study, two observers recorded the lions' behaviors. Observers reached a criterion of 93% interrater reliability. Behavioral observations were recorded using a continuous focal animal sampling method (Altmann, 1974) with a fixed-time duration of 15 min. Thus, each lion was observed separately. During a 15-min observation period, the start time (in seconds) of every change in behavior was recorded. This resulted in a complete record of how the animals spent their time per observation. Observations occurred between 9:00 a.m. and 5:00 p.m. Each lion was observed 10 to 20 times a week for 10 weeks for 829 observations. The order in which the lions were observed, the time of day observed, and day of the week were all counterbalanced. Behaviors were recorded using a 5-in. Psion LZ64 handheld computer (Bournemouth, England) with 34K memory in conjunction with the Observer 2.0 software (Noldus Technologies, 1992). Data regularly were downloaded to a 386 Toshiba (T1200XE) laptop computer (Toshiba, New York, New York).

Twenty-three behaviors were coded and grouped into 10 categories. These categories included the following:

1. Appetitive behavior (locomote, stalk, sniff, eat)
2. Social behavior (play, headrub, groom, copulate)
3. Solitary play (play, rolling)
4. Self-grooming
5. Agonistic behavior (agnostic, object defense, deadlock)
6. Other infrequent actions (shake, paw window, drink, eliminate, other)
7. Rest
8. Stand
9. Pace
10. Not visible to the observer

Standing was recorded as a quadrupedal stance without motion and usually involved focusing on an object or individual. Pacing was defined operationally as a

fixed, repetitive locomotion in a fixed route accompanied by pivot turns. Also recorded were data on temperature and weather conditions.

Fecal Samples

In addition to daily behavioral observations, all feces from all lions were collected for 5 consecutive days every second week of each feeding period for digestibility measurements. The collection of feces for 5 days is a common procedure used for digestibility studies in domestic animals (Association of American Feed Control Officials, 1998) and is designed to overcome variability in daily fecal excretion patterns by individuals. All feces were collected twice daily from the outdoor yard and the night pen. Just prior to feeding, food for each lion was mixed with 14 to 24 g of inert, colored jewelry seed beads to mark individuals. Each lion was fed beads of a different color. The beads were not affected by digestion and passed through to the feces, where they were used to identify the source of the fecal material for the food digestibility study.

Feces were weighed, placed in plastic containers that accumulated the fecal output for each lion for the 5 days, and stored refrigerated. At the end of the fecal collection period, the accumulated feces of each lion was frozen until analyzed. Food samples also were collected every second week during each feeding period and submitted for analysis.

The Association of Official Analytical Chemists (1997) methods were used to analyze food and fecal samples for moisture, protein, and fat. Gross energy was determined by bomb calorimetry. Apparent digestibility percentage was calculated as the concentration of the nutrient in the food minus the concentration of the nutrient in the feces divided by the concentration of the nutrient in the food, times 100.

RESULTS

Figure 1 shows food nutrient digestibility across feeding schedules. Average digestibility of fat, protein, and dry matter for the lions on the conventional feeding schedule was 96.8%, 92.0%, and 81.6%, respectively. Digestibility data were analyzed using repeated measures analyses of variance and post hoc *t* tests ($p < .05$). Digestibility of fat (98.6%), protein (96.4%), and dry matter (91.9%) increased significantly; fat: $F(4, 20) = 13.17, p = .0001$; protein: $F(4, 20) = 17.85, p = .0001$; and dry matter: $F(4, 20) = 4.41, p = .01$, when lions were adapted to the gorge and fast feeding schedule compared to the conventional feeding schedule. In addition, mean food intake expressed as grams per day, as shown in Figure 2, decreased significantly, $F(4, 20) = 4.77, p = .007$, when the

lions were fed the larger, infrequent meals during the gorge and fast schedule compared to the conventional feeding.

Following the conclusion of the 10-week study in September 1993, lions were maintained on the gorge and fast feeding schedule until the end of 1996. Then they were switched back to the conventional feeding schedule to facilitate shifting them between enclosures. Table 1 shows body weights of the lions from before the start of the 10-week study through the next 4 years. A decrease in the body weights of four of the five lions occurred over the period in which the gorge and fast feeding schedule was practiced. Four of the five lions routinely left a portion of each meal uneaten. For half her meals, the fifth lion left small amounts of food. In contrast, no food remained when lions were fed on the conventional schedule of small, daily meals. When conventional feeding was resumed in late 1996, weights for three of

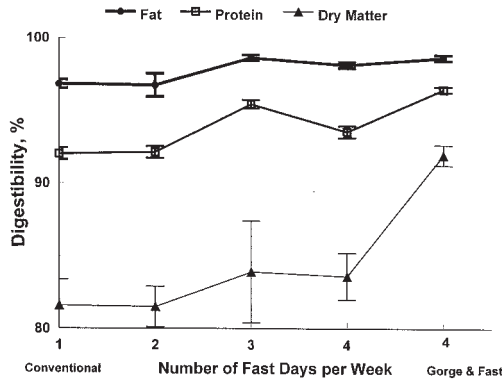


FIGURE 1 Food nutrient digestibility in percentages (and standard deviations) across feeding schedules.

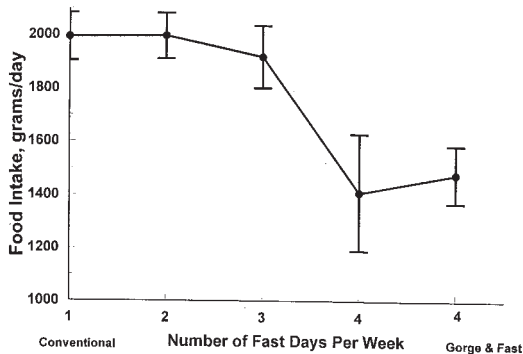


FIGURE 2 Mean food intake (and standard deviations) expressed as grams per day.

TABLE 1
Age (at the Start of the Study) and Body Weights of Lions Prior to the Start
of the 10-Week Study Through 4 Years

<i>Lion</i>	<i>Age^a</i>	<i>May 1993</i>	<i>April 1994</i>	<i>January 1996</i>	<i>May 1997</i>
Arusha	5.75	145.0	5146.3	132.0	NA
Binti	3.75	152.6	146.1	135.7	147.2
Manyara	5.75	156.5	151.5	158.3	133.9
Nanuki	3.75	136.5	171.0	115.7	138.8
Sam	6.75	199.1	NA	167.4	179.1

Note. Body weights given in Kgs. NA = not available.

^aGiven in years.

the five lions again increased. One lion's weight increased in 1996 before the conventional feeding resumed: The lion was under veterinary care for a leg injury. The second lion was euthanized in January 1997 because of neurological problems unrelated to the study.

The proportion of time the lions spent in each behavior per 15-min observation was also calculated. The behaviors then were grouped into five categories:

1. Active (appetitive, social, agonistic, play, grooming, and other active behaviors)
2. Stand
3. Rest
4. Pace
5. Not visible

Overall, under both the conventional and gorge and fast feeding schedules, the lions spent the greatest proportion of their time resting (77% and 72%, respectively) followed by some type of action (11% and 14.3% of the time, respectively). They stood alert 8% and 9% of the time, respectively. The lions paced 3 to 3.7% of the time; 93% of the pacing occurred in the afternoon. When pacing was evaluated according to feeding and fasting days only, lions paced twice as much on feeding days as fasting days (4% vs. 2%). The lions were out of view only 0.9% and 1.2% of the time, respectively.

Separate dependent *t* tests were conducted to compare the conventional feeding schedule (Weeks 1 & 2) with the gorge and fast feeding schedule (Weeks 9 & 10). The two schedules showed no significant differences in the proportion of time the lions rested, $t(4) = 1.290, p = .27$; stood alert, $t(4) = 0.363, p = .73$; were active, $t(4) = 1.703, p = .16$; paced, $t(4) = 0.728, p = .51$; or were not visible, $t(4) = 1.392, p = .24$.

However, because active behavior was an inclusive category and some of the behaviors may have decreased although others increased, the active category was divided back into six smaller categories: appetitive, agonistic, social, grooming, solitary play, and other actions. There was very little agonistic ($< 0.1\%$), play ($< 0.5\%$) or other ($< 0.5\%$) behaviors during either feeding schedule, and the amount of grooming (2%) did not change. Thus, individual dependent *t*s were calculated only for social and appetitive behaviors. There was a significant increase in appetitive behaviors from 6% during conventional feeding to 9% during gorge and fast feeding, $t(4) = 2.685$, $p = .05$. There was no change in social behavior, (2.5% and 2.0%), $t(4) = 0.941$, $p = .40$. Finally, a dependent *t* test was conducted to compare the proportion of time the lions paced on days they were fed versus days they were not fed. The lions paced twice as much on feeding days (4%) as on fasting days (2%), $t(4) = 3.472$, $p = .03$.

DISCUSSION

Switching the five captive lions from conventional feeding to gorge and fast feeding produced small but important effects in their food digestibility and health (as determined by body weight). Feeding lions large infrequent meals on a random schedule resulted in improved digestibility of fat, protein, and dry matter. This suggests that the physiology of large and small cats is not the same and that lions are adapted more to a variable feeding schedule than to a schedule of small frequent meals. In addition, the body weights of four of the five lions decreased to weights common for wild lions (Schaller, 1972). Most likely, the decline in body weight is due to the decrease in food intake and corresponding decrease in calories over the course of the gorge and fast feeding period. Although body weights were not measured consistently across the study period, a change back to conventional feeding resulting in increases in lion body weights suggests that body weights were affected by the gorge and fast feeding patterns. The only lion who did not show a corresponding weight increase—in fact, showed a decrease in weight—was on a weight reducing diet in response to a leg injury.

There were no changes in lion behavior between the two feeding schedules except for a small but significant increase in appetitive behaviors with gorge and fast feeding. In captivity, lions lack the opportunity, available in the wild, to engage in the brief—but intense—exertion related to hunting; therefore, an increase in appetitive behaviors—or other (nonstereotypic) active behaviors—is desirable. To expend the energy they consume without putting on weight, lions need to increase the amount of low intensity activities available in captivity. In addition, an increase in appetitive behaviors lets zoo visitors observe species-typical behaviors. Furthermore, zoo visitors' common perception of excessively inactive captive lions was not substantiated under either feeding schedule. Compared to the

85% of time lions were observed sleeping in the wild (Schaller, 1972), these lions were observed resting 77% and 72% of the time. Finally, contrary to Lyons, Young, and Deng (1997) this gorge and fast feeding schedule, which created animals highly motivated to feed, did not result in unwanted pacing as a response to being unable to satisfy that motivation.

One hypothesis not supported was that pacing would decrease with gorge and fast feeding. Pacing did not differ in the two feeding schedules. However, the data supported the hypothesis that pacing in this group of lions was primarily anticipatory; 93% of all pacing occurred in the afternoon before feeding and was directed at the entrance to the night quarters in which the lions were fed. Thus, we anticipated that randomized feeding days would prevent the lions from anticipating when they would be fed. On feeding days, however, possibly cued by the smell of thawing meat and activities of keeper staff, the lions were twice as likely to pace as on a day they were not fed. This finding of decreased pacing on fast days also is opposite to that of Lyons et al. (1997) who found that felids (tigers, jaguars, leopards, and snow leopards) who were fed every third morning, paced more frequently on fast days than feed days and more frequent immediately after eating than before. Lyons et al. suggested returning large felids to daily feedings. However, the fixedness of a 3-day feeding cycle may have reinforced pacing on a fixed-interval schedule, resulting in increased pacing as the feeding day approached. Furthermore, of the two lions in their study who were fed daily, rather than on the 3-day cycle, one paced frequently. Feedings should be fixed so that feeding days occur irregularly or unpredictably. Perhaps, had the time of day the lions were fed been randomized along with the day of the week, the increase in anticipatory pacing on feeding days in this study may have been further minimized.

One concern over implementing a gorge and fast feeding schedule was the potential increase in agonistic behavior. However, there was no increase in agonistic behavior among the lions. In fact, there were only 33 observations of agonistic encounters across the study period; only two agonistic encounters occurred during Weeks 9 and 10. Even after 96 hr of fasting, lions showed no signs of aggression or discomfort. The general lack of change in behavior demonstrates that zoos can implement important changes in feeding routines affecting the lion's health without affecting behavior.

Although zoos increasingly are creating habitats that are more natural for captive wildlife, some species—especially large, strict carnivores—may require more than structural exhibit changes to elicit a wide range of behaviors and improve health. Lions have diets and feeding patterns hard to duplicate in captivity. However, although live prey feeding may not be a viable option in many zoos, simulating some aspects of natural feeding patterns can mediate some of the common problems of captivity for lions. This study has shown that changing the lions' feeding schedule better to model natural patterns has improved digestibility, reduced

body weight to a more healthy level, and decreased pacing on fasting days without adversely affecting behavior.

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