Improving the Feeding of Captive Felines Through Application of Field Data

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The tactics employed by large felines in food-getting in the wild are contrasted with the conditions which prevail in captivity. While zoos cannot recreate a completely natural existence, there are points at which nature's ways can guide management in improving the quality of life for zoo animals. Equating an adequate diet with good nutrition leads to dietary substitutions which ignore non-nutritive requirements. Among the issues discussed are substitute activities, oral health in relation to food texture, and the psychological aspects of feeding.

Key words: felines, oral health, diet, husbandry, psychological well-being

INTRODUCTION

In 1966 the International Zoo Yearbook published a special section on the nutrition of zoo animals. A frequently referenced paper in that section, by Richard Fiennes, pathologist at the Zoological Society of London, concluded with this statement: “Without adequate feeding there can be little breeding.” The breeding of exotics is clearly a major concern of zoological institutions today, and leads us to a careful consideration of the diverse factors which impinge on fecundity, including its relationship to feeding behavior and diet composition. While Fiennes spoke of several aspects of captive feeding, it is clear when discussing “adequate” diets, his concern was primarily with nutrition.

Zoo personnel universally share in this concern. The nutritional aspects of food dominate our thinking at virtually all levels of management, from the keeper who feeds, to the accountant who keeps a wary eye on costs. The extreme view is that which Hediger, in the symposium referred to above, called the “retort” theory of feeding. This theory holds that if nutritionally adequate food is provided, then good health, increased longevity, and improved breeding will ensue. Hediger himself stands at the other end of the continuum in arguing for a more naturalistic approach. Even he recognized, however, that there is need for substitution and modification of natural diet regimes, given the constraints of a captive existence. Yet a current reading of the
zoo literature leads inexorably to the conclusion that, in our practice of animal management, non-nutritional aspects remain poorly understood, are infrequently studied, and stand as a footnote to concerns with the captive feeding of exotic species. Wackernagel’s [1968] statement of nearly 20 years ago remains as the prevailing view: “We want to make it clear that, in planning diets, the physiological considerations should have priority.”

An example from the captive breeding of cheetahs at the San Diego Wild Animal Park highlights the contention that there is more to food consumption than mere assimilation of balanced quantities of protein, fat, carbohydrates, minerals, and vitamins. A first indication of a broader problem was that individuals being carefully groomed for breeding would often have to be detoured to the hospital for treatment of infections of the mouth and nasal passages. A second indication arose from a study of activity budgets which revealed that cheetahs were virtually inactive day and night, despite having a 4-acre area at their disposal, and that activity consisted primarily of trips between food bowl and resting sites. A third observation was of markedly different reactions to minced, frozen meat as compared to occasional feeding of rabbit, chicken, or ungulate carcasses. In the latter case one sees improved appetites, a greater tenacity about possession of food, and sometimes even bouts of play centered around the carcass.

These observations point to the importance of nonphysiological variables inherent in styles of provisioning and in the palatability of food to improved husbandry and breeding. A review of the activities involved in capturing and ingesting food in the wild state provides a starting point for examining the many ramifications of captive provisioning. Field data for this report are drawn from observations on the tiger, lion, leopard, and cheetah, since these are among the better studied in the wild, though the findings for large felines probably apply in a general way to other cats as well.

THE PREDATORY SEQUENCE

The feeding activity of large felines can be divided into four components: location of prey, capture tactics, the killing act, and behavior at the kill (Fig. 1). Each
component entails a considerable expenditure of effort, and brings into use the appropriate foraging and feeding equipment, i.e., the sensory modalities, the limbs, claws, teeth, and jaws. The total complex of activities involved in food-getting are discussed in light of potential importance to physical and psychological health of felines maintained in captivity.

**Searching for Prey**

Schaller [1967] states that much of the Bengal tiger’s daily activity revolves around its food supply, whether hunting, feeding, or resting satiated beside the remains of its kill. Its usual method of hunting is to walk through its range in search of prey. Hunting primarily at night, the tiger will cover an average distance of 10 to 20 miles during an unsuccessful night of searching. Total energy expended in the location of prey will depend on availability, luck, success rate in capturing, and frequency with which the species must feed. Success rates for tigers at Kanha Park in India were estimated by Schaller to be one kill in every 20 attempts. Once a kill is made, a tiger may feed for 3 to 4 nights, the duration depending on size of prey and number of feeding individuals.

Cheetahs in Nairobi Park, Kenya, averaged 8 km of travel per day according to Eaton [1974], most of this in search of food. Success rates for cheetahs are much higher than for tigers, estimated at from 50-70%. Cheetahs habitually stay with the carcass for a single feeding, if in fact it is not appropriated by other carnivores, as is frequently the case. Solitary cheetahs were estimated by McLaughlin [1970] to make 150 kills per year, on the average.

Being primarily a nocturnal hunter, and the most catholic in diet of the four species here considered, it is less clear how much leopards must work at locating prey. Kill rates for an 8-month period at Seronera were determined by Schaller [1972] to be about one gazelle per week, representing about two-thirds of the total diet.

Lions may key on vultures [Bartlett and Bartlett, 1982] or hyena behavior at a kill [Schaller, 1972] to locate food, thereby reducing search time. Schaller’s detailed descriptions indicate that lions also are notable in the extent to which they wait for quarry to wander within stalking range, as opposed to searching over long distances. However, in areas such as the Kalahari, where prey may be seasonally scarce, searching for food is a major and sometimes fruitless activity [Owens and Owens, 1984]. At his Serengeti study site, Schaller [1972] observed that most kills were made by females, and nearly half of all hunts involved two or more lions. Between 17% and 30% of stalks were successful, the higher rates pertaining when two or more lions hunted together.

According to Caro [cited in Lewin, 1987], a female cheetah with an average litter of three cubs spends 40% of her time searching for prey. Though comparable figures have not been published for the other species under review here, it is clear that the food quest requires a substantial expenditure of energy in all.

**Methods of Capture**

Once prey are located, several tactics may be used in the capture attempt. Those shown in Figure 1 are adapted from Hamilton [1973], and are intended to be all inclusive for predators. Stalking, as the term implies, entails the use of stealth to approach the target to within striking distance. The ambush tactic (Hamilton’s “sentinel”) is one in which the predator takes up a position and waits for prey to approach.
Stealth and camouflage are important to the success of this tactic. While scavenge predation commonly refers to feeding on carrion, Hamilton has in mind active predation, which does not rely on concealment and which is directed at prey which are small and often incapable of rapid flight. Prey in this instance are pursued upon being flushed from cover as the predator openly travels over its range. Coursing (Hamilton’s “group hunting”) is a pack activity such as that used by wild dogs, and depends on long-distance pursuit during which the prey is driven to exhaustion.

The first three tactics are used in varying degrees by large cats, though stalking is more common. Cautious stalks of up to a half-hour or more have been described, followed by a rapid sprint to close the distance on the surprised target. A major difference exists between the cheetah and other large cats in that it depends more on speed than on stealth. Cheetahs have in fact been observed to ignore prey which failed to show flight [Ammann and Ammann, 1985]. Varadaj [1964] clocked by auto a group of five cheetahs running along a dirt road in Bechuanaland at 60 mph, and cites other tests indicating even greater speed. Because of its reliance on speed, the cheetah can begin its capture sprint from distances as great as 300 yards. Field observers consistently report that the cheetah, at the end of its sprint, must rest for about one-half hour before it can begin feeding. While other cats depend less on pure speed, capture by stalking usually entails a series of momentarily exhausting chases before success is obtained, and represents an expenditure of energy which must be added to that spent in locating food.

**Killing Tactics**

The killing bout also differs between cheetahs and other large cats [Kruuk and Turner, 1967]. Using either the dewclaw for tripping or a glancing blow with its forepaw, the cheetah relies on the rapidly fleeing prey’s loss of balance in closing in for the death-bite. Because its jaws are less powerful than those of larger cats [Ewer, 1973], its preferred mode of killing is the throat bite, which induces strangulation. This may require holding down a struggling animal for periods of 5 minutes or more in the case of larger prey. The larger cats use their weight to advantage in dragging down prey and may either suffocate by a throat hold or bite into the nape of the neck, thereby damaging the spinal cord.

All of the cats under consideration commonly drag or carry the carcass some distance before feeding. Suggested reasons are to seek shade or cover, to protect the kill from other predators, or to be near water or a litter of cubs. For the cheetah this is a relatively easy matter, since its preference is for the smaller gazelles or other relatively lightweight prey. The other cats in our sample, on the other hand, may expend substantial effort in relocating before feeding. A tiger estimated to weigh 250 kg has been recorded as dragging a 320-kg sambar a distance of 150 yards [Breeden, 1984]. Schaller [1972] reports adult lions dragging 275-kg zebras, and leopards routinely maneuver kills of up to 70 kg into the safety of trees. Again, it should be noted that the procurement of food is hard work.

**The Consumptive Phase**

Several descriptions of consumption are reported in the literature. As a rule, all the large cats begin at the rear or underbelly, and work forward to the rib cage and forequarters, neck, and head. According to Schaller [1972], lions and leopards will sometimes eat the viscera first, perhaps to satisfy their fat and vitamin requirements.
After opening the skin, the scissorlike action of the carnassial dentition is used to slice through muscle. In addition, the jaws and teeth are used in ripping, pulling, and tearing actions as chunks of flesh are extracted and swallowed with minimum mastication. Estimates of consumption for large cats range as high as 25 kg of meat at one feeding, but a quantity of 10–20 kg is more common. Processing a carcass into ingestible portions places a substantial workload on the jaws and teeth, as does the gnawing on and crushing of manageable morsels of bone and cartilage.

Caching is most common in leopards, the kill being maneuvered into trees even before beginning to feed, or hidden in thickets in treeless areas. Tigers will on occasion cover remaining portions of a carcass with brush and leaves, but reports of caching by lions are doubted by Schaller [1972]. All observers agree that cheetahs make no attempt to retain unconsumed portions of a kill. Whether cached or simply guarded from other predators, vigilance from first to last meal constitutes an additional investment in food procurement.

EUROPHAGY

A final point of relevance to this topic is the diversity of prey consumed in the wild. Preferring prey of not more than 20 kg in body weight, the cheetah specializes in one or two regionally abundant species. Thompson’s gazelles accounted for about 90% of the diet on the Serengeti [Schaller, 1972], while at Kruger National Park 68% of kills were impala [Pienaar, 1969]. Even so, at the latter site, 24 different kinds of prey in a sample of 2,527 kills were recorded.

At Kanha Park the chital deer made up about 50% of the diet of tigers, but Schaller [1967] mentions also birds, langurs, porcupines, even occasional reptiles, amphibians, and fish. In his words, a tiger will eat whatever it can catch.

The Serengeti lions prey mostly on wildebeest, zebra, buffalo, and topi, but in 3 years of study Schaller [1972] observed feeding on 18 different mammals, four birds, and an occasional crocodile. He cites other reports of opportunistic feeding on pythons, catfish, and locusts. Pienaar’s [1969] list for Kruger National Park mentions 40 different prey species.

The leopard is said by both Schaller [1972] and Myers [1976] to be more catholic in diet than any other large cat, and Schaller notes that the food list in the Serengeti included hare, hyrax, various small and medium-sized antelopes, python, several kinds of birds, and several carnivores.

Diversity in prey consumed is probably dictated by regional availability and by opportunity. Whether large felids seek certain kinds of prey out of preference or need is unknown, but all evidence is consistent with the notion that choice is based solely on the possibility of capture.

To summarize, large cats in the wild feed primarily on one or a few species but opportunistically include up to 20–30 different kinds of prey for a given region, indicating that they are anything but monophagous. They often travel many miles in search of food, make numerous unsuccessful attempts at capture, drag carcasses to feeding sites when successful, and with the jaws and teeth parcel up prodigious amounts of flesh at any one feeding.
ISSUES IN CAPTIVE FEEDING

The application of knowledge derived from nature has great potential for improving the quality of life for captive exotics [Markowitz et al., 1978; Hancocks, 1980; Hutchins et al., 1983]. While nature cannot be entirely simulated in zoos, if management regimes meet the objectively measurable criteria of good health, display of ecologically valid behavior, and successful reproduction [Quick, 1984], they will have used field data to good cause. As regards the feeding of felines, nature informs us on several issues for which the substitutions constrained by captivity can be modified to meet these criteria, viz., activity levels, food packaging, and pleasure in food consumption.

Activity

The first three components in the acquisition of food (locating, capturing, and killing) have to do with considerable activity, hence energy expenditure and body conditioning. These are the most radically altered aspects of a captive existence, and zoos have few choices in the matter. But one should recognize that a tremendous void results from their removal, leading to boredom, the appearance of stereotyped behaviors, and generally poor condition. Substitute activities are a partial solution, and notable strides in this direction have been developed by Markowitz [1982]. Though cost is often perceived as a deterrent to “engineered” approaches, in the long run they may be good investments in improved health and vitality.

Food Packaging

The last component of the predatory sequence, behavior at the kill, provides information which is more readily applicable to the captive situation. Field reports of the last two decades contain information on what animals eat, and how they go about it. From nature’s packaging of food items one can extract information about such attributes as texture, taste, temperature, smell, color, and shape. The most convincing evidence of the importance of the non-nutritive properties of carnivore food is in findings on oral health. In response to recurring nasal and mouth infections of cheetahs at the San Diego Wild Animal Park, Fitch and Fagan [1982] conducted a survey which revealed that of 20 cheetahs in U.S. collections which were fed formulated diets, 15 (75%) had focal palatine erosion, i.e., perforation of the palate by the penetrating action of the lower molars. By contrast, 39 individuals fed animal carcasses lacked the condition. Of 22 museum skulls, none of 14 wild-caught had focal palatine erosion, whereas 4 of 8 zoo-raised did (diet unknown). The authors proposed that dental malocclusion as a result of feeding a soft texture diet led to a self-inflicted wounding of the palatine mucosa and bone.

Two additional studies address this issue. The first, by Vosburgh et al. [1982], entailed experimental feeding of soft and hard diets to timber wolves and found that texture of food was a significant factor in the development of dental plaque, i.e., 50% less in those fed a hard diet. A second study, by Haberstroh et al. [1984], measured effects of providing beef femurs to Amur tigers which, when offered twice weekly, clearly improved gingival health and reduced plaque formation. Though still in its early stages, the testing of non-nutritive variables in the matter of carnivore diets favors hard-texture diets as a way of improving oral health, and thus reproductive success and longevity.
Pleasure in Feeding

The contrasting reactions of cheetahs to naturalistic (carcass) and to commercially prepared foods, as noted in the Introduction, suggest issues in palatability and thus in the psychological aspects of feeding which have rarely been objectively examined. Lacking hard data, we address the issue here by analogy. There are several parallels between the ways in which humans and zoo animals forage. Procurement and preparation is in neither case an individual activity, but the task of specialists. For humans, an entire industry exists to take care of nutritional balance, packaging, sterilizing, precooking, preserving, flavoring, etc., all of which greatly reduces forage time at the supermarket, as well as time spent in preparation of food for consumption. In a similar vein, grass for herbivores is pelleted; fruits and leaves for monkeys are chowed; and meat for carnivores is minced, packaged, and frozen, all for similar reasons of nutritional value, cost, and convenience. Like the human, the zoo animal invests little effort in foraging or in the processing of food items for ingestion.

The attention humans give to taste, texture, smell, color, and temperature of food, as well as to the time and place of ingesting, is a measure of the enjoyment derived from feeding. Food that is nutritionally balanced but lacking in those attributes which please the palate is disdained. Caution must be exercised in inferring the gustatory proclivities of animals, but field data do strongly suggest that they find "pleasure" in feeding. While psychological well-being remains an elusive concept, the difficulties encountered in its measurement do not render it unimportant. Until more refined techniques for assessing the mental state of animals in feeding are developed, we may be guided by the fact that the behaviors commonly associated with feeding in nature lead to the conclusion that much of their pleasure centers around food.

It would be impractical to advocate the abandonment of formulated foods. One may question, however, if it is wise to regard them as a complete and adequate solution to captive feeding. Testing with regard to oral health, though just beginning, points to the need for suitable supplementation, and there is reason to believe that as we examine the psychology of feeding with proper experimentation, we will find here as well significant relationships to health and to breeding.

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REFERENCES

Fitch, H.M.; Fagan, D.A. Focal palatine erosion associated with dental malocclusion in captive
Myers, N. The leopard Panthera pardus in Africa. IUCN MONOGRAPH # 5, Morges, Switzerland, 1976.
Wackernagel, H. Substitution and prefabricated diets for zoo animals. SYMPOSIUM, ZOOLOGICAL SOCIETY OF LONDON 21:1–12, 1968.