PROCEEDINGS OF THE NUTRITION SOCIETY

A joint meeting of the Nutrition Society, the Royal Zoological Society of Scotland and the British Federation of Zoos was held at Edinburgh Zoo, Murrayfield, Edinburgh on 16–18 May 1997

Symposium on 'Nutrition of wild and captive wild animals'

Plenary Lecture

Captive wild animal nutrition: a historical perspective

BY ELLEN S. DIERENFELD

Department of Nutrition, Wildlife Conservation Society, Bronx, NY 10460, USA

Proper feeding management of wild animals in captivity incorporates both husbandry skills and applied nutritional sciences. As a basic foundation of animal management, nutrition is integral to longevity, disease prevention, growth and reproduction, yet has received insufficient focus in the zoological community, although somewhat more detailed attention has been paid to free-ranging wildlife, particularly those of economic value to man. The field of nutrition is itself a rather recent scientific discipline. In the nineteenth century the importance of major food constituents such as protein, fat, carbohydrate, and fibre was recognized, and mineral nutrition was receiving much attention. But not until this century has the essentiality of vitamins, fatty acids, amino acids, and many trace elements been demonstrated, with biochemical and molecular characterization of interactions among nutrients still relatively unexplored. Thus, it is not surprising that comparative animal nutrition, focused on zoo and wildlife species, has a relatively short, yet extremely productive and rewarding, history.

Noteworthy and rapid developments in animal nutrition are demonstrated by the fact that twenty revisions of *Feeds and Feeding*, a widely used textbook, were published within the 50-year span following its initial printing in 1898 (Morrison, 1953). Discussions in the earliest editions, of necessity, were based largely on the experience and observations of successful farmers rather than the results of actual experiments. Thus, in the field of wildlife nutrition, qualitative, rather than quantitative, information provided the underlying basis for the development of diets fed to many wildlife species, and studies of food habits have continued as a major percentage of all wildlife nutrition investigations (Robbins, 1993).

While detailed natural history documentation of field biologists supplies a written record of foods consumed by many species, such information with no chemical evaluation of dietary constituents, or assessment of utilization, provides only a partial basis for applied feeding programmes. Dietary choices of free-ranging wildlife are complex chemically, temporally, and spatially, and animals use a wide variety of morphological, physiological, and anatomical adaptations to acquire and utilize foodstuffs. Although we can rarely duplicate ingredients of any animal's diet in a captive feeding situation, what we can duplicate, and must focus on, are the nutrients contained within those diets. Wildlife and zoo nutrition are integrally linked; physiological and biochemical components must be considered as critical as ecological and behavioural considerations in meeting the needs of the species under our care.

EARLY ANIMAL MANAGEMENT

The earliest managers of animal collections, be they of zoos, menageries, or hunting stock, inevitably relied almost exclusively on observed feeding habits and natural history of free-ranging creatures to develop captive diets based on available ingredients; unfortunately, with little or no written records, quantitative or qualitative data, and often with poor health consequences. Duplication of 'natural' diets became an attempted norm, with little regard to nutrient composition, and may have appeared at least marginally adequate for many species maintained in native environments, exposed to natural climatic conditions, exercise regimens, and foodstuffs. As long as additional nutrient stresses were not added (i.e. environmental alterations, disease, reproduction, lactation, or growth), captive animals may have adapted to suboptimal diets for prolonged periods, and such diets became incorporated as a standard. Thus, unsupplemented chunk meat was fed to carnivores, fruits and vegetables to primates and birds, and agricultural grains and hay to herbivores, even with the recognition that diets were not conducive to reproduction, or resulted in malformed offspring (Bartlett, 1899).

Early records from Calcutta Zoo, first published in 1892 and reprinted in 1995, provide diet information also derived from field observations of feeding habits (Sanyal, 1892). Some of these diet records, however, contain subtle yet vital information which may have resulted in more-nutritionally-sound diets for zoo species at the time (given today's knowledge base). For example, prey items (both vertebrate and invertebrate) were offered whole; a variety of locally-caught prey for some species (Ca-deficient beetles along with snails and their Ca-rich shells) also may have proved beneficial. Meat, including bones, was specifically noted for large felids such as tiger, lion, and leopard. Grasses, S, salt, and entrails were included as essential dietary components for numerous carnivores. Specific browses and forages were listed, with scientific nomenclature, as the staple for rhinoceros, elephant, folivorous primates, and fruit bats. Few sweet fruits were found in these diets; more often starchy or fibrous fruits (plaintain, figs (*Ficus carica*)) and/or vegetables were noted. Not all the diets described by Sanyal (1892) appear nutritionally balanced on inspection, and certain detail such as the composition of the 'biscuit' is essential for evaluation. Nonetheless, these early qualitative dietary records can contribute information which may provide useful comparative data if assessed quantitatively.

However, most early animal managers also embraced short-term production goals and options not compatible with the long-term conservation objectives of today's zoos (Conway, 1995), such as maintenance for exhibition purposes only, rather than longevity or reproduction for species survival, with replacement from wild populations considered a viable alternative. We now must design feeding programmes and diets to provide nutritional support for all stages of life, and cannot assume that traditional zoo diets are adequate, even if signs of nutritional imbalance are not immediately obvious. It is precisely this change in zoo objectives, combined with animal housing and environments radically altered from native habitats, that has precipitated much of the more recent intensive investigation into captive wildlife nutrition.

SCIENTIFICALLY-BASED ZOO NUTRITION

The earliest published account of severe metabolic bone disease in zoo species, alleviated through supplementation with bone meal and cod liver oil (Bland Sutton, 1888), was followed by the experimental work of Corson-White (1922, 1931a,b, 1932) in response to osteomalacia observed in zoo primates. At that time, diet was proposed as one possible factor in development of the condition, but mechanisms were not understood and vitamin D

was only just being characterized as an anti-rachitic factor. Diets of cebid monkeys displaying severe disease at the Philadelphia Zoo were evaluated and found to be: (1) low in protein quality and quantity; (2) low in P content; (3) low in fat; (4) very high in soluble carbohydrates; (5) low in ash, and predominantly acid, with only traces of Ca, P, Fe, and low in Na, K, S, and Mg; (6) vitamins A, B, and C were very low or lacking altogether. Individual ingredients (rice, bread, potato, peanuts, bananas, maize, egg, apple, and onion) were fed to rats; no single constituent of the monkey's diet was able to support life and health. The total diet generally resulted in good body condition and reproduction, but litters were always eaten.

An experimental diet was created to correct recognized deficiencies; normal growth and reproduction were restored to the experimental rats, and a revised diet was suggested for the zoo primates, with casein, butterfat, carrots, lettuce, and a salt mixture added to the original diet. By 1931, the exhibition life of primates had increased, but bone lesions were still prevalent (Corson-White, 1931a). Comments by the author suggest some possible underlying reasons: (1) diet changes were never fully adapted; (2) depression in the total amount of summer sunlight was followed in the succeeding year by an increase in the number of bone cases. The influence of sunlight was definite, although variation among primate species in susceptibility seemed apparent. A mixed diet was formulated for primates using nutrient requirements established for man which represented the first published recipe for a nutritionally-based ration fed to zoo species. The baked diet was fed with fresh produce to augment vitamins and add appetite stimulants.

The following annual report of Corson-White (1932) described feeding behaviours of experimental free-ranging monkeys in an attempt to develop an optimal diet based on animal choices, as apparently the mixed ration was not wholly accepted (by care staff rather than animals). The free-ranging cebid monkeys consumed the produce-based diet described previously, along with self-selected whole nestlings, and bone meal used as fertilizer (scraped from the ground). The basal diet was then supplemented with either dog kennel-ration, or a lump of mineral-supplemented ground beef. Following this diet change, vegetables, fruits, and crickets (Acheta domestica) comprised the free-range choices of the monkeys. Thus, a final diet was created based on a combination of animal choice and known nutrient requirements: dog kennel-ration, ground beef or chicken heads alternating with one egg, boiled rice or bread or sweet potato (Ipomoea batata) or peanuts or banana or carrots or beets, with a half pat of butter or a one-quarter teaspoon of cod liver oil ultimately incorporated. Animals markedly improved in general appearance, activity and reproduction, with no evidence of bony lesions. Notably, these monkeys also had access to sunlight daily for 2 years.

This early and promising zoo research concurrent with rapid advances in the livestock, fur, pet, and laboratory animal feed industries, led to the formulated mixed rations that constituted the staple diets for many species in the Philadelphia Zoological Garden (Ratcliffe, 1937, 1940). Numerous omnivorous species including rodents, raccoons (Procyon lotor), bears, and birds were successfully fed on a modified version of Corson-White's (1932) original diet, and Ratcliffe (1937, 1940) assisted with the development and feeding implementation of a mixed meat ration, as well as a composite herbivore ration. Clearly the stage had been set for a new era of feeding zoo animals.

Diets continued to be refined and tested on zoo species, with an emphasis on improved health, disease resistance and feeding economics (Ratcliffe, 1963). Formulas were adapted, incorporating locally-available ingredients and feed manufacturers, for use as concentrate supplements in European facilities. Diets detailed by Wackernagel (1961, 1966, 1968) included herbivore pellets designed to suit the needs of both grazing and browsing species,

fed with dry or fresh forages, omnivore cakes and pellets, supplemented meat mixtures for carnivores, soft-bill-bird feeds, pelleted poultry rations suitable for ducks, geese, cranes and ostrich, colour-feeding rations, and a mineral–vitamin supplement for piscivores. Nutrient compositions of these formulated diets were provided, based primarily on animal agricultural standards of the time and the premise that 'all animals need the same groups of nutrients in similar proportions'.

Proper nutrition as a valuable management tool in zoos was emphasized in vol. 6 and 16 of *International Zoo Yearbook* (Jarvis, 1966; Olney, 1976), and recognition of nutritional diseases in zoo animals became more extensive throughout the 1960s and 1970s as veterinary staff expanded (Fowler, 1978; Wallach & Boever, 1983). Although numerous research institutes and nutritionists collaborated with zoos in Europe and North America during this time, the first professionally-trained staff nutritionists in North American zoos were hired in the mid-1970s, in Europe in the 1980s, and only in 1994 did the American Association of Zoos and Aquariums recognize nutrition as a scientific advisory speciality.

CONCURRENT AND COMPLEMENTARY SCIENCE

Agriculture- and industry-based priorities contributed to primary advances in animal nutrition throughout this same time period (1880s to the present), resulting in the estimated nutrient requirements for most species of domestic and laboratory animals published by the Committee on Animal Nutrition, National Research Council of the US National Academy of Sciences; similar publications are available in other countries. Thus, detailed nutrient recommendations are available for various levels of production in livestock (beef and dairy cattle, goats, horses, poultry, sheep and pigs), different physiological stages in domestic (dogs, cats) and fur-bearing (mink, foxes) animals, as well as laboratory (rabbits, rodents, and primates) species. While the nutrient requirements of most wildlife species remain unknown, extrapolation from domestic models can be useful. Major constituents of foods, their analyses, indications of deficiency and toxicity, and evaluation of diets for zoo and wildlife species can be derived from many general animal nutrition texts, although the cogency of C. T. Robbins (1993) in dealing with this complex topic is unsurpassed.

In the 1960s, commercially-manufactured products developed for laboratory and pet animals were first actively marketed for feeding zoo animals in both Europe and North America. Based on wildlife and range management issues, nutritional studies of black-tailed deer (*Odocoileus hemionus*; Nordan *et al.* 1968), red deer (*Cervus elephus*; Maloiy *et al.* 1968; Haigh & Hudson, 1993), reindeer (*Rangifer tarandus*; Steen, 1968) and captive white-tailed deer (*Odocoileus virginianus*; Ullrey, 1974) resulted in the development of nutritionally-complete pelleted rations successfully fed to a variety of other exotic ruminants, using the domestic sheep as the physiological model. Pellets based on the nutritional requirements of horses were utilized by zebras, wild equids, and a variety of other non-ruminant herbivores. By the 1970s and 1980s, modified livestock, laboratory animal and pet feeds were widely incorporated into zoo and captive wildlife feeding programmes. This economic focus on exotic animal nutrition continues as production-based systems have been applied more recently to improving the dietary husbandry of ratites, camelids, and African game species.

Food diversity studies have not been as historically relevant to agriculture as to wildlife nutrition, given the limited number of feeds and feedstuffs utilized in the feed industry. Many of the chemical correlates of free-ranging animal food choices (such as secondary plant compounds) were first identified, advanced, and developed by wildlife ecologists, entomologists, and field biologists (Robbins, 1993). More recent interest for

agricultural and pharmaceutical application has led to rapid advances in analytical techniques, just as focus on tropical *v.* temperate agricultural feeding systems led to modified methods of chemical analysis and evaluating feed utilization that incorporated differences in species' behavioural and physiological adaptations to native environments, even for well-studied domestic ruminants (see Van Soest, 1994).

Agricultural, behavioural, biochemical and physiological studies focused on both free-ranging and captive species (for numerous examples, see Crawford, 1968; Montgomery, 1978; Hume, 1983; Robbins, 1993; Van Soest, 1994) provided instrumental baseline data from which the integrative disciplines of nutritional ecology and comparative animal nutrition were formed (Martinez del Rio & Cork, 1997). Technological advances in laboratory analyses and physiological monitoring have expanded the capabilities of both field- and laboratory-based scientists to more readily combine specialities to provide valuable information for improving the nutrition and feeding management of captive wildlife. Yet nutritional problems persist in feeding captive wildlife in zoos, possibly from the use of inappropriate domestic animal models, and certainly from a lack of basic information on nutrient composition of dietary ingredients.

LIMITATIONS OF DOMESTIC ANIMAL MODELS

Carnivores

Characteristics and metabolic adaptations of mammalian carnivores were recently reviewed with respect to wildlife species (Allen *et al.* 1996). Also detailed were many of the current nutritional problems seen in zoo carnivores fed on commercial canned, frozen, or dry diets formulated for domestic cats and dogs, including tooth and gum problems from too little abrasive in the diet, obesity, urolithiasis, and possible vitamin A toxicosis.

Unique metabolic adaptations have been documented in domestic cats which influence utilization and dietary requirements for protein, fatty acids, carbohydrates and vitamins (National Research Council, 1986), and set them apart from more omnivorous carnivores. Cats require higher levels of dietary protein, and dietary sources of taurine, arachidonic acid, niacin, and preformed vitamin A compared with dogs. By inference, these adaptations reflect evolutionary differences in food resource utilization, with felids consuming a prey base higher in these nutrients than more omnivorous carnivores. While similar enzymic pathways have not been examined in detail for other strict carnivores including piscivores and insectivores, some interesting speculations and inferences are possible regarding vitamin A nutrition of these feeding classifications based on chemical composition of their food resources.

The vitamin A content of twelve species of whole fish, frozen and stored for 3–9 months, ranged from a calculated 2800 µg/kg DM in rainbow smelt (*Osmerus mordax*) to >72 000 µg/kg DM in mackerel (*Scomber scombrus*; Dierenfeld *et al.* 1991*a*; Wildlife Conservation Society, unpublished results). Although vitamin A requirements have not been established for most wildlife species, Mazzaro *et al.* (1994) suggested a vitamin A requirement of 90–180 µg/d for the northern fur seal (*Callorhinus ursinus*), levels which would be supplied by less than 250 g whole fresh fish. Vitamin A requirements established for wildlife and domestic species range from about 900–4500 µg/kg DM (Robbins, 1993). Assuming the vitamin A requirements of piscivorous species are similar to those of other animals, vitamin A needs would thus appear to be met without additional necessary supplementation of a diet comprising whole fish, provided fish are processed and stored to minimize deterioration.

By contrast, vitamin A content in nine samples of whole invertebrate prey measured averaged only 45 µg/kg DM in waxworms (wax moth (*Galleria mellonella*) larvae) to 720 µg/kg DM in wild-caught earthworms (*Lumbricus terrestris*; D. Barker, E. S. Dierenfeld and M. P. Fitzpatrick, unpublished results). Invertebrates in general appear to be a poor dietary source of preformed vitamin A (Bowers & McCay, 1940; Nestler *et al.* 1949; Jones *et al.* 1972), and feeding high levels of this nutrient may be detrimental, particularly to species which may have evolved no mechanisms of coping with high dietary loads. At least one specialist insectivore, the tamandua (*Tamandua tetradactyla*) appears susceptible to vitamin A toxicosis at dietary levels considered acceptable for domestic carnivores (Dierenfeld *et al.* 1995a). Invertebrates examined do contain carotenoid pigments, with possible vitamin A precursor activity, but mechanisms for converting carotenoids to active vitamin A have not been examined in insectivores.

Furthermore, known antagonistic nutrient interactions among the fat-soluble vitamins may be precipitated by excesses of vitamin A in diets of these species, but remain to be investigated. These two examples, illustrated for a single nutrient, demonstrate our lack of a suitable domestic model for some specialist mammalian carnivore species; even less information is known concerning their appropriateness as the physiological model for other classes of animals.

Herbivores

A broad generalized overview of mammalian herbivore nutrition including digestive tract specializations, selecting an appropriate domestic animal model, and guidelines for evaluating pelleted diets, hays, and browses can be found in Oftedal *et al.* (1996). Most zoo herbivores can be fed rather successfully on dry diets formulated for livestock, comprising agricultural grains and supplemental fresh or dried forages. Exceptions to this statement include species for which perhaps appropriate domestic models have not yet been identified, or diet composition and/or digestive physiological adaptations have not been studied in adequate detail. Specialized browsers, hoofstock with omnivorous feeding habits, tropical herbivores, and very small ruminants are species for which optimal captive diets have not yet been developed. Each of these groups display behavioural selectivity in natural feeding habits which may be difficult to duplicate in captive feeding situations, and which, in turn, may signal physiological adaptations that have not been considered in meeting unknown nutritional requirements (Van Soest, 1996). Relating nutritional properties of foods selected or avoided in nature may provide some useful guidelines in developing more appropriate captive diets for some of these species.

Although its origin of usage in North American zoos is unclear, lucerne (*Medicago sativa*) hay has been widely presented as a substitute browse for many species. The clear physical distinctions of leaves and stems between legume hay and grass hays may underlie its use as a browse, allowing the herbivore to 'self-select' plant parts; however, the chemical distinctions between those same plant fractions truly underlie the suitability of lucerne as a generic browse.

Browse palatability and digestion studies were conducted with penned okapi (*Okapi johnstoni*) in Zaire; in addition, the chemical composition of plants selected (*n* 61) and rejected (*n* 55) by free-ranging okapi was determined (Okapi Metapopulation Workshop, 1996). Both groups of animals appeared to be selecting forage based on total cell wall content, consuming plants containing <500 g neutral-detergent fibre (NDF)/kg DM. Crude protein (N × 6·25) content did not vary between preferred and rejected browses (150–210 g/kg DM); however, the soluble organic fraction (not further characterized) was much

higher in preferred browse compared with rejected browse. Based on these limited chemical components, legume hays fed to okapi in North American zoos (g/kg DM: 440 NDF, 210 protein; Okapi Metapopulation Workshop, 1996) would appear chemically similar and may provide a suitable browse substitute, as would several temperate browse trees analysed. However, legume hays grown in northern Europe are not considered a palatable or nutritionally-adequate browse for the okapi; chemical (hence, nutritional) differences due to growing conditions may certainly underlie these apparent inconsistencies, but data have not yet been summarized.

At the other extreme, the legume hays of North America by no means chemically resemble browses consumed by the black rhinoceros (*Diceros bicornis*; Dierenfeld *et al.* 1995*b*) and contain much higher protein, lower fibre, variable mineral content, and are more digestible than natural diets. Numerous health problems have been reported in this species in captivity, some with a possible nutritional basis (Miller, 1994). Feeding lucerne as the exclusive forage may lead to mineral imbalances, colic and diarrhoea. Recommendations have been made to feed mixed grass–legume hays and/or a mixture of legume and less-digestible browse, and high-fibre-concentrate pellets, with the diet formulated to meet horse nutrient requirements, at least until a more suitable diet is developed.

Clearly, comparison of the chemical composition of native plants consumed by herbivores can give at least a rough starting point in selecting appropriate forage substitutes. The dearth of information on both nutritional and non-nutritive components of native browses available to and utilized in captive feeding programmes globally remains another area of fruitful investigation and untapped resource.

Laboratory species

Most of the detailed research has been conducted on, and nutritional requirements developed for, omnivorous non-human primates (Oftedal & Allen, 1996). Primate food habits range from insectivory (specialized carnivory) to folivory (specialized herbivory); thus, other domestic animals, and/or a combination of species, may provide more suitable physiological models.

Gorillas (*Gorilla gorilla*) pose an interesting nutrition challenge in zoos, having been fed on an omnivorous diet as the only means of keeping them alive more than a few months in captivity (Bartlett, 1899; Hornaday, 1934). Yet cardiovascular disease, ulcerative colitis, and elevated cholesterol levels (2810–3110 mg/l) have been reported as major health factors in zoo gorillas (Cousins, 1979; McGuire *et al.* 1989). In nature, gorillas are vegetarians and consume essentially no animal products (Calvert, 1985; Rogers *et al.* 1990; Tutin & Fernandez, 1993). Fruits consumed by free-ranging gorillas are much more fibrous than our traditional idea of cultivated fruits, and can have the same or even higher levels of dietary fibre as leaves. Thus, diseases reported can be compared with those seen in Westernized human populations consuming high-fat and -protein and low-fibre diets. Gorillas have an enlarged hindgut, with probably an enhanced ability to ferment dietary fibre compared with smaller primates, but no metabolic studies have been conducted on this species. Human dietary allowances established by the National Academy of Sciences (National Research Council, 1989) would probably provide more suitable nutrient guidelines for the gorilla than laboratory primates, but further research must be conducted.

Similarly, dietary requirements of many of the colobine monkeys might be better met using small ruminants as a physiological model, as the foregut of these primates functions in a similar manner. Diets based on nutrient requirements of omnivorous primates

frequently result in diarrhoea, torsion, bloat, or other gastrointestinal upsets in zoo colobines (Nijboer & Dierenfeld, 1996). Foods eaten by free-ranging colobines contain much higher levels of dietary fibre than diets fed in zoos, and lower available protein concentrations than recommended for non-human primate models. Additionally, mineral concentrations in natural foods are within ranges considered more suitable for ruminant herbivores than primates (Yeager *et al.* 1997). The combination of field- and captive-animal-based studies provides specific insight into nutrient composition of foods which may assist in diet development for improved animal management.

Laboratory rodents as models again represent a very limited physiological and behavioural range of diets and digestive adaptations compared with those displayed among the Rodentia, ranging from almost total carnivory (for example, grasshopper mouse (*Onychomys leucogaster*)) to large fermenting herbivores (for example, capybara (*Hydrochoerus capybara*)). The two most common laboratory rodents, in fact, have different dietary habits, with mice more granivorous and rats, omnivorous. Nonetheless, both are used extensively as feed for numerous carnivores, and are often reared on generic 'rodent' diets.

Two recent publications (Douglas *et al.* 1994; Clum *et al.* 1996) suggest that the nutrient composition of the diet has a significant impact on the ultimate body composition of the rodent, just as has been documented for numerous livestock species. Although these diets may be suitable for maintaining the species for which they were originally developed, we have unintentionally altered the production goals of those diets, resulting in nutritionally-imbalanced feeds for secondary consumers. Detailed information on the nutrient composition of free-ranging prey would thus provide dietary guidelines for application to both primary and secondary consumers.

Avian models

Domestic poultry species for which published nutrient requirements exist are limited to granivorous species, including chickens, turkeys, geese, ducks, pheasants and quail. Dry pelleted rations developed for chickens were suggested as satisfactory for finches, canaries, and other small caged birds as early as the 1950s (Coffin, 1953). However, growth and feeding trials to quantify nutrient intakes and requirements of these species and psitticines did not appear in the scientific literature until considerably later (Roudybush & Grau, 1986; Earle & Clarke, 1991; Ullrey *et al.* 1991). Much of the lack of published data regarding psitticine nutrition, in fact, may reflect the proprietary nature of research conducted by commercial feed manufacturers. Although information is limited, the nutrient densities of diets fed to growing precocial birds appear adequate to support normal growth of the altricial species studied; far more research is needed before broader generalizations can be made. Poultry nutrient requirements at least provide a baseline from which to begin dietary evaluations for many avian species.

Exceptions to the use of poultry as a model for birds, however, are numerous. Hummingbird nutrient requirements, based on nectar characteristics and food selection, have been investigated in some detail (Brice & Grau, 1989, 1991). The protein requirement of this specialist feeder (about 50–100 g/kg DM) is much reduced compared with the more omnivorous poultry models.

Similarly, disaccharide enzyme systems of frugivorous birds have been studied in detail, and shown to vary phylogenetically (Martinez del Rio, 1990), which may also be associated with differences in dietary habits. The pulp of most bird-dispersed fruits tends to be rich in glucose and fructose with small amounts of sucrose, while those of fruits

cultivated for human consumption are higher in sucrose. Feeding preferences, both in captive and free-ranging habitats, may thus signal the presence of specific enzymic pathways for carbohydrate digestion (Martinez del Rio & Stevens, 1989) which in turn provides information on suitable dietary ingredients. Significantly, many frugivorous birds in captivity also accumulate significant hepatic Fe stores, some pathological (Dierenfeld *et al.* 1991*b*). Although a number of nutrient interactions may be involved in development of this disease, including simply high dietary Fe levels and/or enhanced absorption of Fe when fed with ascorbic acid, it is possible that inappropriate dietary carbohydrates may also contribute (Fields *et al.* 1993).

Nutrient requirements of carnivorous birds, however, should perhaps be modelled on known metabolic adaptations of domestic obligate carnivores, the other end of the metabolic spectrum. Cats lack glucokinase (*EC* 2.7.1.2) and preferentially use amino acids for gluconeogenesis (National Research Council, 1986); recent studies suggested similar enzymic adaptations in the owl (*Tyto alba*; Klasing & Myers, 1996) and black vulture (*Coragyps atratus*; Migliorini *et al.* 1973) as compared with the omnivorous chicken. Other unique enzyme systems of the Felidae have not been examined systematically in comparison with carnivorous birds; anecdotal information suggests fat-soluble vitamin nutrition may be another rewarding topic of comparative investigation.

FUTURE DIRECTIVES

Numerous nutritional deficiency diseases in zoo and wildlife species have been identified and reported, generally as medical case reports rather than experimentally-controlled studies. More recently, nutritional excesses, antagonisms and frank toxicities are appearing in the literature. While unique nutrient requirements and metabolic adaptations of some exotic species have been determined, for the most part, we are still in the early stages of understanding and appropriately meeting the nutritional needs of many species under our care. A combination of basic and applied research is essential, conducted on both free-ranging and captive animals; thus, a cross-disciplinary approach must continue. Qualitative information on natural feeding habits, in combination with quantitative data on food nutrient composition and utilization, can provide direction for development of optimal diets for captive animal management.

REFERENCES

Allen, M. E., Oftedal, O. T. & Baer, D. J. (1996). The feeding and nutrition of carnivores. In *Wild Mammals in Captivity*, pp. 139–147 [D. G. Kleiman, M. E. Allen, K. V. Thompson and S. Lumpkin, editors]. Chicago: The University of Chicago Press.

Bartlett, A. D. (1899). *Wild Animals in Captivity*, 3rd ed. London: Chapman & Hall.

Bland Sutton, J. (1888). Rickets in monkeys, lions, bears, and birds. *Journal of Comparative Medicine and Surgery* 10, 1–29.

Bowers, R. E. & McCay, C. M. (1940). Insect life without vitamin A. *Science* 92, 291.

Brice, A. & Grau, C. R. (1989). Hummingbird nutrition: development of a purified diet for long-term maintenance. *Zoo Biology* 8, 233–237.

Brice, A. & Grau, C. R. (1991). Protein requirements of Costa's hummingbirds *Calypte costae*. *Physiological Zoology* 64, 611–626.

Calvert, J. (1985). Food selection by western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia* **65**, 236–246.

Clum, N. J., Fitzpatrick, M. P. & Dierenfeld, E. S. (1996). Effects of diet on nutritional content of whole vertebrate prey. *Zoo Biology* **15**, 525–537.

Coffin, D. L. (1953). *Angell Memorial Parakeet and Parrot Book*. Boston: Angell Memorial Animal Hospital.

Conway, W. G. (1995). The conservation park: a new zoo synthesis for a changed world. In *The Ark Evolving Zoos and Aquariums in Transition*, pp. 257–276 [C. M. Wemmer, editor]. Front Royal: Smithsonian Institution Conservation and Research Center.

Corson-White, E. P. (1922). Osteomalacia. *Archives of Internal Medicine* **30**, 620–628.

Corson-White, E. P. (1931*a*). Degenerative bone disease in primates. *Report of the Laboratory and Museum of Comparative Pathology, Zoological Society of Philadelphia*, pp. 31–35. Philadelphia, PA: Zoological Society of Philadelphia.

Corson-White, E. P. (1931*b*). Diet of primates. *Report of the Laboratory and Museum of Comparative Pathology, Zoological Society of Philadelphia*, pp. 35–37. Philadelphia, PA: Zoological Society of Philadelphia.

Corson-White, E. P. (1932). Diet in relation to degenerative bone lesions and fertility. *Report of the Laboratory and Museum of Comparative Pathology, Zoological Society of Philadelphia*, pp. 26–28. Philadelphia, PA: Zoological Society of Philadelphia.

Cousins, D. (1979). Mortality factors in captive gorillas. *International Zoo News* **30**, 5–17.

Crawford, M. A. (editor) (1968). *Comparative Nutrition of Wild Animals. Symposia of the Zoological Society of London* no. 21. London: Academic Press.

Dierenfeld, E. S., Barker, D., McNamara, T. S., Walberg, J. A. & Furr, H. C. (1995*a*). Vitamin A and insectivore nutrition. *Verhandlungsbericht Erkrankungen Zootiere* **37**, 245–249.

Dierenfeld, E. S., du Toit, R. & Braselton, W. E. (1995*b*). Nutrient composition of selected browses consumed by black rhinoceros (*Diceros bicornis*) in the Zambezi Valley, Zimbabwe. *Journal of Zoo and Wildlife Medicine* **26**, 220–230.

Dierenfeld, E. S., Katz, N., Pearson, J., Murru, F. & Asper, E. D. (1991*a*). Retinol and α-tocopherol concentrations in whole fish commonly fed in zoos and aquariums. *Zoo Biology* **10**, 119–125.

Dierenfeld, E. S., Pini, M. T. & Sheppard, C. D. (1991*b*). Hemosiderosis and dietary iron in birds. *Journal of Nutrition* **124**, 2685S–2686S.

Douglas, T. C., Pennino, M. & Dierenfeld, E. S. (1994). Vitamins E and A, and proximate composition of whole mice and rats used as feed. *Comparative Biochemistry and Physiology* **107**A, 419–424.

Earle, K. E. & Clarke, N. R. (1991). The nutrition of the budgerigar (*Melopsittacus undulatus*). *Journal of Nutrition* **121**, S186–S192.

Fields, M., Lewis, C. G., Lure, M. D., Burns, W. A. & Antholine, W. E. (1993). Low dietary iron prevents free radical formation and heart pathology of copper-deficient rats fed fructose. *Proceedings of the Society for Experimental Biology and Medicine* **202**, 225–232.

Fowler, M. E. (1978). *Zoo and Wild Animal Medicine*. Philadelphia: W. B. Saunders.

Haigh, J. C. & Hudson, R. J. (1993). *Farming Wapiti and Red Deer. St Louis, MO: Mosby*.

Hornaday, W. T. (1934). *Official Guide Book to the New York Zoological Park*. New York: New York Zoological Society.

Hume, I. D. (1983). *Digestive Physiology and Nutrition of Marsupials*. Cambridge: Cambridge University Press.

Jarvis, C. (editor) (1966). *International Zoo Yearbook* **6**, 3–115.

Jones, I. D., Cooper, R. W. & Harding, R. S. (1972). Composition of mealworm *Tenebrio molior* larvae. *Journal of Zoo Animal Medicine* **3**, 34–41.

Klasing, K. C. & Myers, M. R. (1996). Comparative tolerance and metabolic adaptations to glucose of the barn owl (*Tyto alba*) and chicken (*Gallus domesticus*). *Symposia of the Comparative Nutrition Society* **1**, 78–80.

McGuire, J. T., Dierenfeld, E. S., Poppenga, R. H. & Braselton, W. E. (1989) Plasma alpha-tocopherol, retinol, cholesterol, and mineral concentrations in captive gorillas. *Journal of Medical Primatology* **18**, 155–161.

Maloiy, G. M. O., Kay, R. N. B. & Goodall, E. D. (1968). Studies on the physiology of digestion and metabolism of the red deer (*Cervus elaphus*). In *Comparative Nutrition of Wild Animals. Symposia of the Zoological Society of London* no. 21, pp. 101–108 [M. A. Crawford, editor]. London: Academic Press.

Martinez del Rio, C. (1990). Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. *Physiological Zoology* **63**, 987–1011.

Martinez del Rio, C. & Cork, S. (1997). Exploring nutritional biodiversity: a society is born. *Trends in Ecology and Evolution* **12**, 9–10.

Martinez del Rio, C. & Stevens, B. R. (1989). Physiological constraint on feeding behavior: intestinal membrane disaccharidases of the starling. *Science* **243**, 794–796.

Mazzaro, L. M., Dunn, J. L., Furr, H. C. & Clark, R. M. (1994). Vitamin A plasma tracer kinetics in northern fur seals (*Callorhinus ursinus*) using 3,4-didehydroretinol as a tracer. *Proceedings of the International Association for Aquatic Animal Medicine Conference*, Vallejo, CA. Abstr. Baltimore, MD: IAAAM.

Migliorini, R. H., Linder, C., Moura, J. L. & Veiga, J. A. S. (1973). Gluconeogenesis in a carnivorous bird (black vulture). *American Journal of Physiology* **225**, 1389–1392.

Miller, R. E. (1994). Diseases of black rhinoceroses in captivity. In *Rhinos as Game Ranch Animals*, pp. 180–185 [B. L. Penzhorn and N. P. J. Kriek, editors]. Onderstepoort, South Africa: Wildlife Group of the South African Veterinary Association.

Montgomery, G. G. (editor) (1978). *The Ecology of Arboreal Folivores*. Washington, DC: Smithsonian Institution Press.

Morrison, F. B. (1953). *Feeds and Feeding*, 21st ed. Ithaca, NY: The Morrison Publishing Company.

National Research Council (1986). *Nutrient Requirements of Cats*, revised ed. Washington, DC: National Academy Press.

National Research Council (1989). *Recommended Dietary Allowances*, 10th ed. Washington, DC: National Academy Press.

Nestler, R. B., Derby, J. V. & Dewitt, J. B. (1949). Vitamin A and carotene content of some wildlife foods. *Journal of Wildlife Management* 13, 271–274.

Nijboer, J. & Dierenfeld, E. S. (1996). Comparison of diets fed to southeast Asian colobines in North American and European zoos, with emphasis on temperate browse composition. *Zoo Biology* 15, 499–508.

Nordan, H. C., Cowan, I. McT. & Wood, A. J. (1968). Nutritional requirements and growth of black-tailed deer, *Odecoileus hemionus columbianus*, in captivity. In *Comparative Nutrition of Wild Animals. Symposia of the Zoological Society of London* no. 21, pp. 89–96 [M. A. Crawford, editor]. London: Academic Press.

Oftedal, O. T. & Allen, M. E. (1996). The feeding and nutrition of omnivores with emphasis on primates. In *Wild Mammals in Captivity*, pp. 148–157 [D. G. Kleiman, M. E. Allen, K. V. Thompson and S. Lumpkin, editors]. Chicago: The University of Chicago Press.

Oftedal, O. T., Baer, D. J. & Allen, M. E. (1996). The feeding and nutrition of herbivores. In *Wild Mammals in Captivity*, pp. 129–138 [D. G. Kleiman, M. E. Allen, K. V. Thompson and S. Lumpkin, editors]. Chicago: The University of Chicago Press.

Okapi Metapopulation Workshop (1996). *Okapi Metapopulation Workshop*. Yulee: White Oak Conservation Center.

Olney, P. J. S. (editor) (1976). *International Zoo Yearbook* 16, 1–70.

Ratcliffe, H. L. (1937). Nutrition. *Report of the Penrose Research Laboratory, Zoological Society of Philadelphia*, pp. 28–30. Philadelphia, PA: Zoological Society of Philadelphia.

Ratcliffe, H. L. (1940). Diets for a zoological garden: some results during a test period of five years. *Zoologica* 25, 463–472.

Ratcliffe, H. L. (1963). Adequate diets for captive wild animals. *Bulletin of the Penrose Research Laboratory, Zoological Society of Philadelphia*, 2nd ed, pp. 1–16. Philadelphia, PA: Zoological Society of Philadelphia.

Robbins, C. T. (1993). *Wildlife Feeding and Nutrition*, 2nd ed. San Diego, CA: Academic Press, Inc.

Rogers, M. E., Maisels, F., Williamson, E. A. Fernandez, M. & Tutin, C. E. G. (1990). Gorilla diet in the Lope Reserve Gabon: a nutritional analysis. *Oecologia* 84, 326–339.

Roudybush, T. E. & Grau, C. R. (1986). Food and water interrelations and the protein requirement for growth of an altricial bird, the cockatiel (*Nymphicus hollandicus*). *Journal of Nutrition* 116, 552–559.

Sanyal, R. B. (1892). *A Handbook of the Management of Wild Animals in Captivity in Lower Bengal*. Calcutta: Bengal Secretariat Press (reprinted by Central Zoo Authority in 1995).

Steen, E. (1968). Some aspects of the nutrition of semi-domestic reindeer. In *Comparative Nutrition of Wild Animals. Symposia of the Zoological Society of London* no. 21, pp. 117–128 [M. A. Crawford, editor]. London: Academic Press.

Tutin, C. E. G. & Fernandez, M. (1993). Composition of the diet of chimpanzees and comparison with that of sympatric lowland gorillas in the Lope Reserve, Gabon. *American Journal of Primatology* 30, 196–211.

Ullrey, D. E. (1974). Nutrition of herbivores in the zoo. *American Association of Zoo Veterinarians Annual Proceedings*, Atlanta, GA, pp. 170–177. Philadelphia, PA: AAZV.

Ullrey, D. E., Allen, M. E. & Baer, D. J. (1991). Formulated diets versus seed mixtures for psitticines. *Journal of Nutrition* 121, S193–S205.

Van Soest, P. J. (1994). *Nutritional Ecology of the Ruminant*. Ithaca, NY: Comstock Cornell University Press.

Van Soest, P. J. (1996). Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biology* 15, 455–480.

Wackernagel, H. (1961). *Modern Methods of Feeding Wild Animals in Zoological Gardens*. Basle: F. Hoffmann-La Roche & Co. Ltd.

Wackernagel, H. (1966). Feeding wild animals in zoological gardens. *International Zoo Yearbook* 6, 23–37.

Wackernagel, H. (1968). Substitution and prefabricated diets for zoo animals. In *Comparative Nutrition of Wild Animals. Symposia of the Zoological Society of London* no. 21, pp. 1–12 [M. A. Crawford, editor]. London: Academic Press.

Wallach, J. D. & Boever, W. J. (1983). *Diseases of Exotic Animals*. Philadelphia: W. B. Saunders Company.

Yeager, C. P., Silver, S. C. & Dierenfeld, E. S. (1997). Mineral and phytochemical influences on foliage selection by the proboscis monkey (*Nasalis larvatus*). *American Journal of Primatology* 41, 117–128.