4

Nutrition in Captivity

Mary E. Allen, PhD and Olav T. Oftedal, PhD

INTRODUCTION

The goal of animal nutrition is the provision of nutrients in sufficient amounts to permit optimal growth and reproduction, as well as reduction of nutrient-related health risks. These consequences are interrelated, since impaired growth and reproduction are often early signs of dietary imbalance. Only in cases of severe or prolonged dietary imbalance are frank deficiency signs normally encountered.

Unfortunately, nutrient deficiency is not unusual in captive green iguanas. For example, metabolic bone disease is a commonly seen problem that may be related to inadequate dietary calcium, inverse calcium:phosphorus ratios, and/or low intakes of dietary vitamin D_3 (cholecalciferol). Inadequate exposure to ultraviolet-B light (UV-B; 280–320 nm) plays an especially critical role in green iguanas.

Another problem thought to relate to nutrient intake is visceral and/or articular gout entailing the deposition of uric acid in soft tissues and in joints, respectively. Since uric acid is the principal nitrogenous waste product in terrestrial reptiles such as iguanas, it has been suggested that pathologic deposition of urates outside the urinary tract may be a consequence of excessive nitrogen loads, perhaps coupled with an increase in blood solutes during dehydration and impaired renal function.

Digestive disorders, including bloat, diarrhea, and torsion, may also reflect inappropriate diet, especially if iguanas are fed diets of such low fiber content that hindgut fermentation is abnormal. Intestinal blockages that occurred in juvenile Galapagos land iguanas (Conolophus subcristatus)¹ were believed to be due to excessive but infrequent feeding of fibrous plant material, and the same may occur in green iguanas.

Most of the descriptions of nutrient deficiencies or

toxicoses in zoo and exotic animals come from clinical case studies. This is true for mammals and birds as well as for reptiles.²⁻⁶ Yet few experimental studies have tested the effects of specific nutrients on reptiles, including iguanas, and the diagnosis of deficiency or toxicosis is typically based on analogous pathologic findings for domestic mammals or birds. There is great risk of error in this approach, especially when a detailed evaluation of nutrient intakes is not undertaken. For example, the assertion that excessive amounts of dog or cat food will produce soft tissue mineralization in reptiles due to high vitamin D levels³ fails to recognize that most dry dog and cat foods are not particularly high in vitamin D (being lower than many products marketed specifically for reptiles), that soft tissue mineralization may be associated with vitamin D deficiency rather than toxicity, and that the greatest cause of vitamin D deficiency may be a lack of UV-B light exposure, rather than dietary vitamin D levels (see discussion below). We are not aware of any controlled studies indicating that dog or cat foods are harmful to reptiles per se. Anecdotally, two Chinese box turtles (Cuora flavomarginata) in our care have been fed a diet of canned cat food (with small amounts of fruit) for 3 years to determine if they would develop signs of nutrient deficiency or toxicity, but so far both appear normal.

In this chapter we review the importance of nutrients such as protein, fiber, calcium, phosphorus, and vitamin D. These may often be imbalanced in the diets fed to green iguanas by pet owners or zoo keepers and may be associated with clinical problems. The importance of ultraviolet light for vitamin D synthesis is also discussed. Unfortunately, relatively few scientific studies have addressed these issues, and most of the data are buried in conference reports and theses, or have yet to be published. We hope that the synthesis of this information will be helpful in the

evaluation and improvement of diets and husbandry of both zoo and pet iguanas.

TRADITIONAL SALAD-TYPE DIETS

Green iguanas are herbivorous in the wild, eating a variety of leaves, fruits, and flowers (see Baer, Chapter 3). It is, therefore, common to offer iguanas a salad-type diet that includes leafy greens, various vegetables, and fruits. Insects, small vertebrates, and other sources of animal protein are sometimes added. In the 1980s iguanas at the National Zoological Park were maintained on a "reptile salad" that was made by mixing chopped fruits and vegetables with soaked dog food kibble. Although the animals appeared to be in good condition, two of four iguanas developed bleeding oral lesions. Close observation revealed that the hard centers of otherwise soft, soaked kibble would lodge between the tongue and palate, a problem that was corrected by longer soaking. However, if dog or other dry foods are soaked excessively, soluble nutrients such as some vitamins may leach out and not be consumed.

One of the problems of a salad-type diet is that animals can self-select among the food items, and the food items chosen may not be nutritionally complete. This is most likely when diets are fed in excess amounts and much of the food is not eaten, or when large groups of animals are fed together and the dominant individual can choose from the large volume of food presented. Unfortunately, there is little evidence that captive animals presented with an array of foods make sound nutritional choices, especially if some of the foods offered are particularly palatable. For example, an iguana selecting mostly soft fruit such as bananas, apples, and grapes will have an inadequate intake of calcium.

Attempts are often made to compensate for nutritional inadequacies in salad-type diets by application of a vitamin-mineral supplement. A supplement will only counter a deficiency if the concentration of the nutrient in the supplement is appropriate and if the correct amount of supplement is ingested. In a typical salad-type diet it is not practical to monitor how much of the supplement adheres to the food actually ingested and, hence, supplement use is almost always guesswork. Although healthy green iguanas may self-select a calcium source such as oystershell if it is offered separately, it is not known if this behavior results in a balanced diet.8 In one study, vitamin D-deficient iguanas decreased calcium intake even though the animals were probably in negative calcium balance.8

Another problem with salad-type diets is that the commercial fruits and vegetables used are apt to be quite different in nutrient composition from the foods eaten in the wild. Since humans prefer low-fiber foods, most types of produce in the marketplace contain relatively low fiber levels, typically about 5–28% neutral-detergent fiber (NDF)^{9–10}, as compared to more than 25% NDF in most of the foods eaten in the wild. ^{11–13} Commercial fruits are also typically low in calcium and protein, so that high fruit diets are apt to be deficient in these and other nutrients (see below). Leafy greens and other vegetables may have a place in iguana diets, but in and of themselves are no replacement for a nutritionally complete food.

THE DEVELOPMENT OF IGUANA DIETS FOR USE IN CENTRAL AMERICA

In general, it is difficult to ascribe success or failure in iguana husbandry to diet due to the inadequacy of diet records, limited information on amounts consumed, variation in solar or fluorescent exposure, and repeated changes in other aspects of husbandry, such as enclosure design, temperature, humidity, and number of cage mates. Thus the opportunity in 1986 to begin nutritional consultation with a large-scale iguanarearing project at the Smithsonian Tropical Research Institute (STRI) in Panama was very welcome. 12,14-16 The overall project, entitled "Alternatives to Destruction," was funded by the W. Alton Jones Foundation with the objective of developing local use of renewable forest resources as an alternative to widespread deforestation of tropical rain forests. Local farming projects included rearing iguanas for meat, farming pacas, and developing forest vegetable gardens. The declines of native iguana populations in Central America had been attributed both to deforestation and overhunting, since many local peoples prized iguana meat and eggs taken from gravid females. 17 If iguana-rearing proved feasible and economical, it might not only reduce pressure on wild populations, but could also serve as the basis for community-oriented economic programs and the development of a wildlife management ethic. The model developed by Dr. Dagmar Werner, director of the green iguana project, involved captive-breeding of females, artificial incubation of eggs, and the headstarting of young animals on artificial diets until they reach sufficient size to deter postrelease predation. Forest patches would serve as iguana pastures, and the farmers would tend and value the forests as sources of iguana meat, fruits, and building materials.

The success of this project depended, in part, on

finding an economical means of feeding hatchlings and juveniles. The logistics and cost of acquisition, refrigerated storage, and processing of a multitude of ingredients for salad-type diets for thousands of iguanas were clearly prohibitive. In preliminary trials, Dr. Werner had determined that the growth rates of iguanas fed on various meal-type ingredients such as soybean meal, meat-and-bone meal, and fish meal were very different. Our first objective was the development of a meal-type diet that would be nutritionally complete. At the time, zoo keepers and curators were skeptical that green iguanas would accept a dry diet, since their only experience had been with the use of salad-type diets. The iguana diets we formulated were similar in ingredients to pelleted rabbit or horse feeds, but contained higher levels of several nutrients that were labile or that might be needed in higher amounts by iguanas, such as proteins and vitamins A, C, D, and E. We were concerned that a pelleted diet might be difficult for hatchlings to consume, whereas the meal form could be ingested by both licking and biting. Dr. Werner reported good acceptance and improved growth on the first diets tested. Subsequently a variety of diets were developed to test growth and physiologic responses to different levels of nutrients such as protein, fiber, calcium, and vitamins in iguanas maintained in Panama, Costa Rica (where the colony subsequently moved under the auspices of the Fundacion Pro Iguana Verde), and at the National Zoological Park. These results, some of which have been published, 8,12,16,18-23 form the basis for much of this chapter.

COMMERCIAL DIETS FOR GREEN IGUANAS

Many owners of pet iguanas experience the frustration and disappointment of iguanas that fail due to nutritional disorders. One is reminded of the former popularity of dime store turtles (mostly hatchling redeared sliders, Trachemys scripta elegans) that would live a few months before perishing of soft shell, inappetence, weakness, and tetany. In the 1950s and 1960s the public did not realize that the dried insects being marketed as turtle food, such as dried ant pupae, were poor sources of calcium and some other nutrients. The lesson to be learned, that a food marketed for a pet reptile is not necessarily nutritionally suitable, is still valid. How many millions of hatchling turtles died of frank calcium deficiency then, or how many young iguanas perish each year from metabolic bone disease now, are not known.

The surge in ownership of pet iguanas following

release of the movie Jurassic Park has been accompanied by a proliferation of commercial iguana feeds. some from reputable feed manufacturers with staff nutritionists and others from pet suppliers with little expertise in diet formulation. The advantage of a processed or manufactured diet is that it can be formulated to contain all nutrients known to be needed by the target species, but the disadvantage is that if any nutrients are omitted or included at inappropriate levels, the damage to captive iguanas may be substantial, especially if other foods are not being offered to them.

Realizing that no regulatory agency is regularly scrutinizing either the composition of or advertising claims for iguana feeds, we obtained and chemically analyzed 31 different diets that were labeled for use for green iguanas (Oftedal, Christopher, and Allen, 1997, unpubl. data; Table 4.1). These samples were obtained in an opportunistic fashion from pet shops and suppliers, and do not address container-tocontainer or batch-to-batch variation of each product. These products were obtained in 1997; some may no longer be manufactured or their formulations may have been changed. Nonetheless, they provide a snapshot of diets available at the time.

Commercial iguana diets may be frozen, canned, pelleted, extruded, or in a meal or powder form. A guaranteed analysis is provided with the diet label, but may be misleading. For example, we found that one manufacturer (Zoo Med, San Luis Obispo, CA) produced two diets, Iguana Food, Juvenile Formula and Iguana Food, Adult Formula. The guaranteed analysis for the juvenile diet was a minimum of 24% crude protein, while that for the adult diet was a minimum of 12%. By analysis, both diets complied with these specifications, as they exceeded the minimum levels, but in fact both diets contained about 27% crude protein on a dry matter basis (DMB). Someone wishing to feed a low-protein diet to adult iguanas would be misled by these labels. A more serious instance was a powdered diet (Zoo Menu Iguana Food, Juvenile Formulation; Zoo Med Laboratories, San Luis Obispo, CA) that was labeled as containing a minimum of 23% protein, but by analysis contained only 12.3% crude protein on a DMB. This discrepancy was also noted by Donoghue²⁴ who reported a value of 14.0% crude protein. However, among diets we studied this was exceptional; most of the diets contained levels of protein and fat similar to or in excess of the guaranteed minima.

Guaranteed analyses are presented on an as-sold (or fresh weight) basis (FWB), but this is not the most useful means of comparing different diets. Two diets with very different water content, such as a

Table 4.1 Composition of manufactured iguana diets available via pet stores.1

Canned 75.0 ± 0.51 1.31 ± 1.06 13.4 ± 3.83 11.1 ± 1.89 2.01 ± 0.17 0.89 ± 0.14 $(n = 3)$ $(70-78)$ $(0.2-3.4)$ $(7-21)$ $(8-14)$ $(1.72-2.31)$ $(0.69-1.15)$	Diet Type	Moisture (%)	Crude Fat (%)	Crude Protein (%)	Acid Fiber (%)	Calcium (%)	Phosphorus (%)
Canned 75.0 \pm 0.51 1.31 \pm 1.06 13.4 \pm 3.83 11.1 \pm 1.89 2.01 \pm 0.17 0.89 \pm 0.14				法的诉讼任务 医全体性现象 网络拉拉斯斯特拉斯 医二甲甲烷酸盐	27.1.24 下級人物上的研究。由成的企業體的等例		
(n = 3) $(70-78)$ $(0.2-3.4)$ $(7-21)$ $(8-14)$ $(1.72-2.31)$ $(0.69-1.15)$	Canned	75.0 ± 0.51	1.31 ± 1.06	13.4 ± 3.83	11.1 ± 1.89	2.01 ± 0.17	0.89 ± 0.14
	(n = 3)	(70–78)	(0.2–3.4)	(7–21)	(8–14)	(1.72–2.31)	(0.69–1.15)

¹Diets were purchased from pet stores or pet store suppliers and include products marketed by American Reptile Inc. (Dry Ridge, KY), Feather Gourmet (Sacramento, CA), Five Star Reptile Foods (Riverview, FL), Fluker Laboratories (Baton Rouge, LA), Kaytee Products (Chilton, WI), L/M Animal Farms (Pleasant Plain, OH), Mill Creek Farms, Ocean Nutrition Corp. (San Diego, CA), Pretty Bird International (Stacy, MN), Premium Nutritional Products (Topeka, KS), Tetra Terrafauna (Reed's) (Morris Plains, NJ), Zeigler Bros./Farnam Companies (Gardners, PA), and Zoo Med Laboratories (San Luis Obispo, CA). N refers to numbers of diets analyzed. Data are presented as mean ± sem, with the range in parentheses. Moisture was determined by oven-drying, fat by extraction with petroleum ether in Soxhlet extractors, protein by the Kjeldahl procedure (TN x 6.25), acid fiber by the Van Soest acid-detergent fiber procedure, and calcium and phosphorus by atomic absorption spectroscopy and the molybdovanadate method, respectively, after digestion in perchloric and nitric acids. Values except moisture are expressed on a dry matter basis.

²Dry refers to diets that were pelleted, extruded, meal-type, or in powder form.

canned diet and a dry-pelleted diet (see Table 4.1), will have very different protein levels on a FWB, but on a DMB the relative amounts of protein may be quite similar. Since captive animals can alter food intake to maintain energy intake, and hence eat more of high-water diets, the amount of protein an animal receives is related more to the percent of protein in the dry matter than the percent protein on FWB. The concentrations of nutrients on a DMB can be calculated as follows:

Nutrient content (DMB) =

100-Nutrient content (FWB)
(100-moisture content)

Unfortunately, the maximum moisture levels guaranteed on the label of iguana foods are not very precise. By analysis, iguana diets contain on average about 5% less water than the declared maximum. If it is not possible to determine moisture directly by analytic drying, we recommend using the average values in Table 4.1 for the type of food: 80% for frozen diets, 75% for canned diets, and 5% for dry diets.

Even on a DMB, there were large differences among manufactured iguana diets (see Table 4.1). For example, protein levels varied from 7 to 30%, fat from 0.2 to 7.5%, acid detergent fiber from 5 to 21%, calcium from 0.9 to 3.7%, and phosphorus from 0.4 to 3.2% (see Table 4.1). Such variations can affect the health and performance of green iguanas, as discussed below.

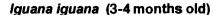
THE REQUIREMENT FOR DIETARY PROTEIN FOR GROWTH

Protein is often a limiting dietary constituent for herbivores because relatively large amounts are needed for tissue growth, whereas the amounts of protein in most parts of most plants are relatively modest. In the wild, reptilian herbivores may be able to maximize protein intake by selecting plant parts high in protein (such as young leaves) or plant species that have relatively high-protein contents (such as legumes). Animals with insufficient protein intakes are apt to have retarded rates of growth, higher susceptibility to disease and impaired reproduction. Therefore, it is of considerable practical importance to determine the protein requirements of green iguanas and to assure that diets meet these needs.

Hatchling green iguanas appear to be particularly sensitive to the concentration of dietary protein. In collaboration with Dr. Dagmar Werner at STRI in Panama, we measured the growth responses of hatchling iguanas when fed diets formulated to vary in protein concentration but to be similar in levels of other nutrients. The ingredient composition and vitamin and mineral premixes in the diets were similar to those in the medium fiber diet reported by Baer et al.,²³ except that the amounts of corn meal, soybean meal, and alfalfa meal were varied to produce target protein levels of 17, 22.5, and 28% (DMB), and supplemental methionine was added to maintain a balance of essential amino acids. By analysis, these

diets contained 0.67, 1.1, and 1.4% lysine, 0.24, 0.33, and 0.36% cystine, and 0.43, 0.48, and 0.59% methionine (DMB), respectively. Each diet was fed in three cages containing 10 hatchlings each.

These diets were fed from hatching until an age of 3-4 months (Figure 4.1). Animals fed diets containing 17% protein (DMB) exhibited poor growth and were both smaller and lighter at the end of the study than were animals fed higher protein diets. The best growth performance occurred with the highest protein level tested, 28% (see Figure 4.1). We conclude that hatchling green iguanas require more than 22.5% protein for maximal growth; but since intermediate protein levels were not tested, we do not



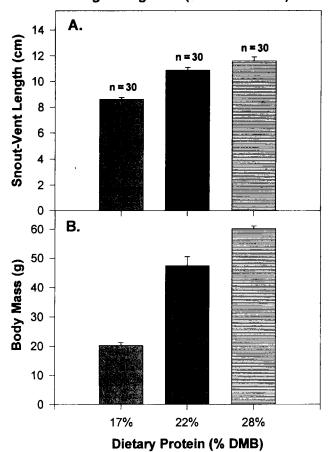


Figure 4.1 The effect of dietary protein on snout-vent length and body mass in young green iguanas. The iguanas were housed and fed in groups of 10 to which they were assigned after hatching. Although all animals were fed the experimental diets from shortly after hatching until an age of 3-4 months, the ages of iguanas when measured varied due to the spread of hatch dates. Data from O. Oftedal, D. Werner, and M. Allen, 1987, unpublished.

know whether animals fed an intermediate protein level, such as 26% protein, would grow at a slower rate than those fed 28% protein. These results reflect diets with a balanced amino acid pattern; even higher protein might be required for maximal growth if any of the essential amino acids were limiting. Higher protein concentrations may also be needed if diets are high in potassium, since terrestrial reptilian herbivores use nitrogen to excrete excess potassium in the form of potassium urates.^{26,27} Conversely, measured protein requirements are usually lower in mammals when the diets are made of highly digestible proteins, such as egg or milk proteins, and the same is likely true in reptiles.

Rapid growth was a primary goal of the iguanarearing program in Panama, since early achievement of large size makes an early release of young iguanas possible, thereby reducing both the cost of feed and the amount of labor required. Hobbyists and zoo staff may not require maximal iguana growth, however, and some fear that rapidly growing animals might manifest behavioral or anatomic abnormalities. However, we are not aware of any adverse consequences associated with rapid growth in iguanas, and did not observe any in our studies. Juvenile iguanas reared on 28% protein diets had high survival rates after release.

DO HIGH-PROTEIN DIETS LEAD TO GOUT?

Another concern is whether there are harmful effects of diets that are too high in protein. In terrestrial reptiles the predominant waste product from protein catabolism is uric acid, which circulates in the blood primarily in ionic form as urate. In the kidneys, urate is both filtered from the blood in the glomeruli and secreted in the tubules.²⁸ Urate excretion plays an important role in electrolyte balance because the urates that precipitate as nitrogenous wastes are largely potassium and sodium urates, with the former predominating in herbivorous lizards.29 It has been shown in both chuckwallas (Sauromalus obesus) and desert tortoises (Gopherus agassizii) that the amounts of urates excreted increase as dietary potassium increases. 26,27 Thus urate excretion depends on both protein and electrolyte intakes.

The concern about urate synthesis and excretion stems from the prevalence of visceral and articular gout in iguanas and other lizards. Visceral gout involves precipitation of urates on a variety of tissues and membranes, especially the liver, kidneys, and the pericardial sac and is usually only noted postmortem. 30 Articular gout is usually progressive, in-

volving painful accumulations of urates in the vicinity of joints, and does not normally resolve upon therapy. Frye³⁰ acknowledged the importance of renal failure (and hence failure to excrete urates) as a principal cause of visceral gout in reptiles, but suggested that visceral gout may also derive directly from high protein intake. We are unaware of any controlled studies that substantiate this claim in reptiles. Ullrey et al.31 argue that amino acid deficiency and imbalance are much more likely responsible for elevated circulating urate levels and gout in birds than is a high protein intake. Insectivorous geckos are also susceptible to gout, even though they normally excrete urates in large amounts without complication. Thus it is not so much whether urates need to be excreted but whether they precipitate in an abnormal way that determines whether gout appears. If the precipitated urates in iguana gout are monosodium urates, as in human gout, possible links to electrolyte status may also warrant investigation.

The causes of both visceral and articular gout are likely multiple, complicating efforts to relate gout to dietary constituents such as protein, amino acids, or purines. For example, gout may be secondary to renal insufficiency or to dehydration. Reduction in dietary protein bears the risk of metabolic disturbance

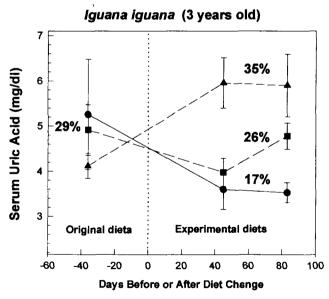


Figure 4.2 The effect of dietary protein on serum uric acid (urate) levels in 3-year-old iguanas. Iguanas were switched from diets containing 29% protein to either higher (35%) or lower (17% and 26%) dietary protein levels, and after about 80 days on the new diets fasting iguanas were bled for serum uric acid determination. The difference in serum urate levels among diets was statistically significant. Data from M. Allen, R. Montali, and O. Oftedal, 1995, unpublished.

due to inadequate amino acid intakes and is a reasonable therapeutic response to observed gout only if it actually results in a decline in circulating urate levels. To examine the relationship of circulating urate levels to dietary protein we switched 24 subadult green iguanas at the National Zoological Park from diets containing 29% crude protein on a DMB to diets containing either 17, 26, or 35% crude protein, and maintained them on these diets for about 80 days. Changes in circulating serum urate levels were evident (Figure 4.2): the lower dietary protein level led to a drop in circulating urate levels, whereas the higher dietary protein level led to an increase. However, even the highest urate levels observed were not very high, being within the typical range reported for fed, hydrated reptiles (1-8 mg/100 ml), birds (3-10 mg/100 ml), or humans (3-7 mg/100 ml).30,32-34 Although much higher levels (up to nearly 30 mg/100 ml) have been observed in some reptiles, these usually reflect postprandial rises in carnivorous species or renal dysfunction. 35,36

PROTEIN LEVELS IN PRACTICAL DIETS

Growth studies suggest that practical diets marketed for juvenile green iguanas should contain at least 22% protein and preferably 26% or more protein on a DMB. Of the 11 commercial diets that we assayed that were labeled for juvenile iguanas, only 4 contained more than 22% protein on a DMB, and one product (Zoo Menu Juvenile Iguana Food; Zoo Med, San Luis Obispo, CA) contained only 12% protein which appears to be too low for normal growth (see Table 4.1). This is consistent with the very low growth rates of juvenile iguanas observed in studies in which this product has been fed. 24,37 However, Hamdoun and Fry³⁷ noted somewhat better growth for four iguanas fed Nutri'guana (Feather Gourmet. Sacramento, CA) that contains only 14% crude protein. Low growth has also been reported for iguanas fed Land Turtle and Iguana Food (Tetra Terrafauna, Morris Plains, NJ) which contains about 12% (our data) or 14% protein²⁴ on a DMB. It is important to remember that commercial diets are highly variable in a wide range of nutrients (see Table 4.1), any of which may influence performance as may palatability and voluntary food intake. To be certain that a commercial diet contains at least 22% protein on a DMB, the guaranteed minimum protein level should be no less than 4.5% for a frozen diet, 5.5% for a canned diet, and 21% for a dry-type diet.

Further evidence is needed to establish a link be-

tween high protein and gout. However, it may still be prudent to reduce dietary protein for reptiles suffering from articular gout or renal disease, and for older animals that are at risk of developing these conditions. We believe that diets containing 15–17% crude protein (DMB) should provide sufficient protein to meet the maintenance protein needs of adult, nonreproductive iguanas, while reducing serum urate levels. It is not known if even lower protein levels can be safely fed for long periods of time

The divergent goals of promoting growth of juvenile iguanas while moderating serum urate levels of adult, nonreproductive iguanas suggest that different diets may be appropriate for iguanas at different stages of life. Of the commercial diets we assayed, 10 were marketed specifically for adult iguanas. These diets ranged in protein concentration from 7 to 28% (DMB), but 7 of the 10 contained 14-16% (Oftedal, Christopher, and Allen, 1997, unpubl. data). Most of these were dry-type diets with guaranteed crude protein levels of 12-14%. Although these levels might be too low to support high egg production, they may be suitable as maintenance rations for adult animals.

FIBER IN IGUANA DIETS

Fiber is found in the thickened cell walls of plants, and as such provides both rigidity and resilience in structures such as stems, leaves and flowers. Herbivores in the wild often consume diets that are quite high in plant fiber. For example, van Marken Lichtenbelt¹³ observed that the foods consumed by green iguanas in a semiarid habitat on Curacao averaged 16-20% acid-detergent fiber (ADF), which was only slightly lower than the average (20–25% ADF) in the available food. Like many herbivores, iguanas rely on symbiotic microorganisms in the hindgut to digest by fermentation the fibrous constituents that the digestive enzymes of vertebrates are unable to attack.9,11,38-39

Fiber comprises various chemical constituents, such as cellulose, hemicellulose, and lignin, that can be separated by specific analytic methods. 11,40,41 Neutraldetergent fiber (NDF) isolates the cell wall containing cellulose, hemicellulose, and lignin, while ADF isolates just the cellulose and lignin. However, a less precise fraction termed crude fiber has legal regulatory definition and is thus the declared fiber constituent in guaranteed analyses of pet foods. The crude fiber technique was developed in the last century as an approximation of the indigestible residue in foods, but it fails to distinguish characteristics of fiber that relate to its

digestibility by symbiotic microorganisms. 40 In iguana diets crude fiber tends to parallel, although at a lower level, the concentration of ADF. For example, three iguana diets formulated to contain 11, 16, and 20% ADF were found to contain 6, 9, and 12% crude fiber, respectively.²³ The guaranteed crude fiber levels in manufactured diets provide an approximate indication of the ADF or cellulose-plus-lignin.

Maintenance of normal digestive function in the hindgut requires that sufficient amounts and types of fibrous constituents be available to support the microbial population. However, this fermentation may become rampant if disrupted by a sudden influx of rapidly fermentable substrates, such as sugars and starches, leading to excessive gas production. acidosis, and bloating. Although captive iguanas can survive on low-fiber diets, we recommend that sufficient fiber be included in the diet to reduce the risk of digestive disorders. The amount of crude or ADF needed to maintain normal digestive function in the green iguana is not known, but by analogy to other herbivores, a minimum acid-fiber level of 10% (or about 6% crude fiber) is recommended.

There is also concern that iguanas as reptilian herbivores may not be able to tolerate very high fiber levels, due to a low rate of fiber fermentation and a relatively unspecialized digestive system. The many small teeth with sharp cusps and the scissorlike motion of the jaws of iguanas are adaptations to the shearing of plant material, but relatively little particle-size reduction occurs through chewing. 42 Bjorndal et al.⁴³ demonstrated the importance of particle size to digestion in aquatic turtles, presumably because small particles have a greater surface area for attack by microbial enzymes. Even when a feed based on ground materials is fed, Baer et al.23 found that an ADF of 20% (about 12% crude fiber) caused a reduction in energy retention and body mass gain by young (2-3 years) iguanas, with the net result that the iguanas had to consume considerably more food for each gram of body weight gained (Figure 4.3). It is likely that green iguanas are even less efficient when whole plant materials are ingested. While it is not clear that there are adverse health consequences of this inefficiency, the limited ability of iguanas to deal with fiber suggests that diets with 20% or more ADF may not be well utilized by young iguanas and should be avoided. It is possible that adult iguanas are more tolerant of high fiber levels, but even in the wild iguanas appear to avoid high-fiber foods. 13 Contrary to the popular view that animals in the wild are in harmony and optimal health, wild animals may have considerable difficulty in obtaining a nutritionally adequate diet. 10

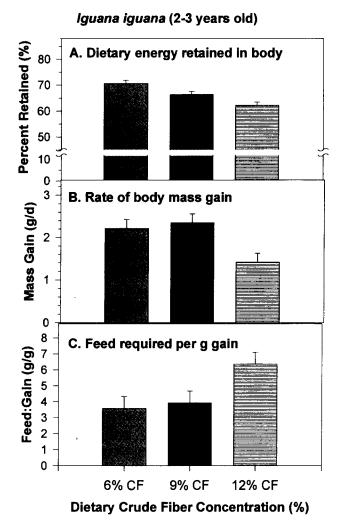


Figure 4.3 The effect of dietary fiber concentration on the amount of energy retained, body mass gain, and feed efficiency of 2–3-year-old iguanas. Each bar represents the mean of 24 animals. Data from Baer et al.²³

CALCIUM METABOLISM AND METABOLIC BONE DISEASE

Metabolic bone disease is a common occurrence in captive green iguanas, both among pets and in zoos, 3,5,6,30,44-46 although the purported causes have rarely been substantiated in controlled studies and should be viewed with caution. Unfortunately some assertions have been repeated so frequently, despite a lack of rigorous evidence, that they are widely accepted and form the basis for dietary recommendations and clinical therapies.

In fact, metabolic bone disease is a collection of pathologic states involving calcium and phosphorus metabolism and bony tissue. In vertebrates circulating calcium levels are normally tightly regulated by

the interacting effects of several regulatory hormones that influence calcium absorption from the digestive tract, calcium excretion in the kidneys, and calcium deposition and withdrawal from bone, the major repository of calcium in the body.⁴⁷ Long-term imbalances in calcium deposition versus withdrawal, whether due to dietary deficiency or hormonal imbalance, produce pathologic changes in bone. The involvement of diverse nutrients, metabolites, hormones, and organs provides the opportunity for a wide range of etiologies of both nutritional and nonnutritional origin. For example, renal disease may influence the 1hydroxylation of calcidiol (25-hydroxy-vitamin D₃), thereby altering concentrations of the active metabolite calcitriol (1,25-dihydroxy-vitamin D₃), synthesis of calcium-binding protein, intestinal uptake of calcium, circulating levels of parathyroid hormone and calcitonin, activity of osteoblasts and osteoclasts, mobilization of calcium from bone, and extent of bone mineralization—all of which might be erroneously attributed to calcium deficiency. Although nonnutritional causes of bone disease are beyond the scope of this paper, it is prudent to remember that a rigorous diagnosis of nutritional deficiency (or toxicity) implies that nutrient intakes have been evaluated in relation to nutrient requirements or tolerances and that alteration of nutrient intakes has been shown to resolve the condition.

Metabolic bone disease (MBD) is further complicated by the diverse pathologic conditions that have been described. Much of the terminology and understanding of processes are derived from human and domestic animal medicine,^{4,48} and the extent to which reptilian disease is similar in origin and outcome remains to be clarified.²

Nutritional secondary hyperparathyroidism results from the overproduction of parathyroid hormone (PTH). This hormone regulates calcium homeostasis by stimulating calcium mobilization from bone and regulating calcium and phosphorus uptake and excretion. In hypocalcemia caused by chronic dietary calcium or vitamin D insufficiency, the parathyroid gland attempts to compensate by releasing PTH which calls for calcium mobilization from bone. Eventually rickets or osteomalacia result.⁴⁹ In humans with primary (nonnutritional) hyperparathyroidism, soft tissue calcification is seen as a result of rapid elevation of serum calcium. Supersaturation of calcium and phosphorus in body fluids occurs and results in calcium phosphate crystal deposition in soft tissues.⁴⁸

Fibrous osteodystrophy has been associated with chronic calcium and/or vitamin D insufficiency and/or calcium:phosphorus imbalances in mammals. This

condition is characterized by the replacement of bony tissue with connective tissue (cartilage). "Big head" in horses and "rubber jaw" in canines, primates, and lizards are commonly reported clinical manifestations.4 In iguanas an increased diameter of the long bones of the limbs is commonly observed.⁴⁴ The specific etiology of this condition is not well understood. It is thought that due to the structural defect of the bone, the body attempts to compensate for the removal of mineral matrix by replacement with connective tissue.

Rickets is the term used to describe the lack of mineralization of bone matrix in growing animals and includes widening of the epiphyseal plate and metaphyses, spontaneous fractures, decreased bone ash, and decreased bone density. The condition has been produced in controlled experiments in which diets low in calcium but adequate in phosphorus have been fed to growing geckos and iguanas^{50,51} and is widely recognized and characterized in mammals, including humans. 48,52

Osteomalacia is a condition of mature bone in which the rate of mineral resorption is faster than the rate of mineralization. The bone becomes soft and shows increased osteoid deposition at stress points, such as at tendon insertions, bone angulations, and curvatures. Bowed long bones, folding fractures, loss of bone density, and thin cortices are seen radiographically. In animals, both rickets and osteomalacia result from inadequate dietary calcium, an inverse ratio of calcium:phosphorus in the diet, and/or inadequate exposure to sunlight in the face of inadequate dietary vitamin D.4

Metastatic mineralization (extraskeletal calcification) of soft tissue has been described in reptiles, including green iguanas. 2,53-55 Mineral appears in fibroelastic tissues, specifically the tunica media and tunica intima of arteries and may be seen radiographically. Renal tubules, lungs, the liver, skeletal muscle, and intestines may also accumulate mineral. Richman et al.⁵⁴ confirmed by alizarin red stain that the foci of mineral in green iguana tissues contained calcium. In humans, irreversible calcification of soft tissues occurs in hypervitaminosis D. Hypercalcemia, muscular weakness, joint pain, and demineralization of bone may also occur. In many cases vitamin D intoxication is fatal.⁵⁶ However, in green iguanas we found extremely low circulating concentrations of the principal vitamin D metabolite (calcidiol) in animals with extensive calcification of soft tissues. 21,53 In addition, these animals had pathologic fractures of long bones and demineralized bone. An indirect method of

evaluating PTH activity, monitoring cyclic AMP in iguana plasma incubated with cultured bone cells, did not indicate high PTH levels, suggesting that soft tissue calcification was not due to hyperparathyroidism in these animals.⁵⁴ Although the pathogenesis of soft tissue calcification is not well understood, these data suggest that this syndrome may reflect vitamin D deficiency rather than vitamin D toxicity in green iguanas. Given this evidence, it is not appropriate to diagnose vitamin D toxicity when soft tissue calcification is seen in reptiles unless supporting evidence such as very high dietary vitamin D and circulating calcidiol levels are available (see below).

These conditions, collectively termed metabolic bone disease, originate as disturbances in calcium, phosphorus, and vitamin D metabolism due to dietary imbalance.4 Many cases undoubtedly result from grossly inadequate diets, such as diets based on fruits, grains, muscle meat, or insects, all of which are often very low in calcium (e.g., <0.3%) of dry matter) and have skewed Ca:P ratios (e.g., <1:2). While the exact calcium and phosphorus requirements of growing green iguanas have not been determined, they are probably similar to mammalian herbivores which have a requirement of 0.5-0.7% Ca and 0.3-0.4% Pon a DMB.41 Growing leopard geckos (Eublepharis macularius) require more than 0.61% calcium (but no more than 0.85% calcium) on a DMB to maintain positive calcium balance.⁵⁰ Egg production may entail even higher requirements given that green iguanas produce on average of 35-43 eggs per clutch that may represent 30-40% of body mass. 57 Given that calcium and phosphorus availability may be reduced by other dietary constituents (such as oxalates and phytates), we recommend that diets should contain at least 1.1% calcium and 0.6% phosphorus on a DMB. For example, thousands of juvenile and reproductive iguanas in Panama and Costa Rica have been fed various mealtype diets containing 1.4–1.8% calcium and 0.5–0.8% phosphorus without presenting clinical signs of MBD. These animals were housed outdoors with solar exposure. Most commercial iguana diets contain 1.5% or more calcium (see Table 4.1), although three dry diets (from one manufacturer) had levels of 0.8-0.9% calcium and inverse Ca:Pratios. The three frozen diets all had very high phosphorus levels and inverse Ca:P ratios (see Table 4.1).

CAN DIET PROVIDE SUFFICIENT VITAMIN D?

An appropriate level of dietary vitamin D is much more difficult to determine, and yet may be critical in that both deficiency and toxicity result in abnormal calcium and phosphorus metabolism, and long-term feeding of vitamin D levels as low as 4000 IU per kg diet can produce toxicity in some animals.⁵⁸ The National Research Council⁵⁸ considers 2200 IU/kg as the safe upper limit for diets for cattle, horses, sheep, and swine.

Vitamin D was initially classified as a nutrient although it is now known that it is a precursor for a steroid hormone, calcitriol, that binds to nuclear receptors and affects gene transcription. This hormone plays a central role in the regulation of calcium and phosphorus uptake and metabolism; in vitamin D deficiency animals have a reduced capacity to absorb dietary calcium and become calcium depleted. If exposed to sufficient UV-B radiation, most terrestrial vertebrates apparently synthesize enough vitamin D and its metabolites to maintain calcium homeostasis.⁵² Indeed, few natural foods contain much vitamin D.⁵⁹

However, if removed from exposure to sunlight or artificial sources of UV-B radiation, animals require an external source of preformed vitamin D. Most appear to be able to use dietary sources, although in domestic poultry and some New World primates vitamin D₂ (ergocalciferol, found in some irradiated plants) is much less potent than vitamin D3 (cholecalciferol, synthesized in irradiated animal skin). Since vitamin D

can be toxic, the effects of long-term ingestion of supplemental vitamin D are of concern and in need of further study.⁵⁹ Excessive UV-B exposure is also damaging to epidermal cells, although in animals that have been studied this is not due to vitamin D toxicity. For a comprehensive review of vitamin D in captive animals see Ullrey and Bernard.60

The thousands of green iguanas raised in Panama and Costa Rica were fed diets containing 2000–3000 IU/kg (DMB), but these animals received direct exposure to tropical sunshine. When animals derived from the same colony were kept indoors at the National Zoological Park without exposure to UV-B radiation for 2 years, about one-fourth of them died with histologic evidence of MBD. Most of the remaining animals were found by radiography to have pathologic fractures of long bones in the limbs, even though these animals were fed diets of very similar nutrient composition, including about 3000 IU/kg vitamin D₃ (Figure 4.4). 18,21 Bone demineralization was confirmed by reduced concentrations of calcium and ash in fat-free dry bone of animals that died, as compared to iguanas kept outdoors and fed nutritionally complete diets in Costa Rica (Figure 4.5). However, the diagnosis was complicated by evidence of calcification of soft tissues such as the aorta, car-

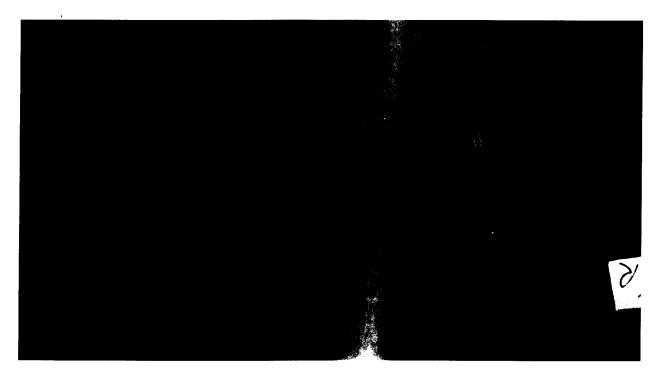


Figure 4.4 Radiograph of a green iguana revealing a comminuted fracture of the right femur. The dense vertical bars represent cerclage wires used to secure femoral fragments. This animal had been maintained on a diet containing about 3000 IU/kg vitamin D3 but had not received exposure to ultraviolet-B radiation for about 2 years. Radiograph courtesy of L. Richman, Department of Pathology and M. Bush, Department of Animal Health, National Zoological Park.

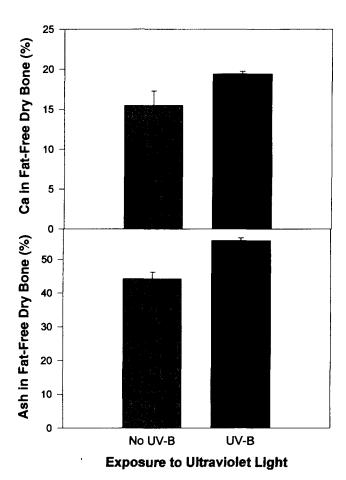


Figure 4.5 Comparison of the calcium and ash concentrations in femurs of green iguanas that were maintained indoors without exposure to ultraviolet-B radiation (no UV-B) for about 2 years, or that were maintained outdoors with exposure to full sunlight in Costa Rica (UV-B). The bones were dried and extracted overnight with petroleum ether prior to ashing; the ash was solubilized in hydrochloric acid prior to measurement of calcium by atomic absorption spectrometry. Data from Oftedal and Jayawickrama, 1995, unpublished.

diac muscle, and gastric mucosa (Figure 4.6), which at the time seemed analogous to signs of vitamin D toxicosis in domestic animals.

Analysis of the circulating concentrations of calcidiol, the most abundant circulating metabolite of vitamin D and an indicator of vitamin D status⁵² revealed extremely low concentrations in the animals that had not been exposed to UV-B radiation for 2 years (Figure 4.7). All 10 animals tested had less than 5 ng/ml calcidiol, and of these seven had undetectable (<1 ng/ml) levels.²¹ By comparison, two iguanas in outdoor enclosures in Costa Rica averaged nearly 150 ng/ml, while four iguanas in outdoor enclosures at the Honolulu Zoo had more than 400 ng/ml (the highest



Figure 4.6 Photomicrograph of cardiac muscle in a green iguana revealing myofiber degeneration and extensive calcification. The iguana had been maintained on a diet containing about 3000 IU/kg vitamin D_3 but had not received exposure to ultraviolet-B radiation for about 2 years. Photomicrograph courtesy of L. Richman, Department of Pathology, National Zoological Park.

level measurable in the assay run). Many of the same animals that had become vitamin D-deficient had previously been used in fluorescent light exposure studies, at which time they had had very high circulating calcidiol levels (see Figure 4.7). When nine surviving vitamin D-deficient animals were exposed to experimental fluorescent bulbs with high UV-B output, circulating calcidiol levels increased rapidly, from less than 8 ng/ml to an average of 299 ng/ml after 27 days.²⁰

It is remarkable that green iguanas could not sustain circulating levels of vitamin D metabolites even though they were consuming diets that were very high (3000 IU/kg) in vitamin D. The vitamin D lev-

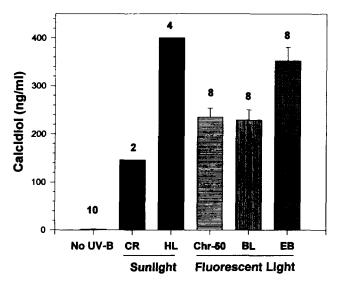


Figure 4.7. Comparison of serum concentrations of the vitamin D metabolite calcidiol (25-OH cholecalciferol) among iguanas maintained with different exposures to ultraviolet-B radiation. The different exposure histories are as follows: No UV-B— no exposure to UV-B for about 2 years; CR—outdoor cages in Costa Rica with exposure to full sun; HL-outdoor cages at the Honolulu Zoo with exposure to full sun; Chr-50-indoor cage with two General Electric Chroma-50 bulbs mounted immediately above cage; BL-indoor cage with one General Electric blacklight and one Chroma-50 bulb mounted immediately above cage; and EB-indoor cage with one Sylvania 2096 experimental bulb and one Chroma-50 bulb mounted immediately above cage. Error bars represent standard errors. No error bars are indicated for HL animals because all animals tested were higher than the highest standard (>400 ng/ml). Data from Allen et al.21

els in the diets were confirmed by both chemical (HPLC) and biologic (rat line test) tests (Oftedal, 1991, unpubl. data), so the possibility of a manufacturing error, such as omission of vitamin D from the vitamin premix, can be discounted. The vitamin D requirements of other animals that have been studied range from 140 to 2500 IU/kg,²¹ although some primates may benefit from higher levels.⁶¹ It appears that green iguanas are unable to utilize dietary vitamin D, at least when supplied at normal levels of fortification. However, some vitamin D is absorbed when large doses are given orally.²⁰ Given the well-known toxicity of large doses of vitamin D in other species, frequent administration of large doses is not advisable.

We conclude that green iguanas maintained without exposure to UV-B radiation are extremely susceptible to vitamin D deficiency, and it is likely that clinical signs appear even more quickly when lowcalcium diets are fed, or when animals are removed from ultraviolet exposure at a very young age. Most of the 31 commercial diets that we assayed appeared to contain sufficient calcium (>1.1%), as long as they are not diluted with great amounts of low-calcium foods, such as most fruits, meat, or insects. However, it is unlikely that any of them contain sufficient vitamin D to prevent the onset of MBD.

THE CRITICAL IMPORTANCE OF ULTRAVIOLET-B LIGHT

In green iguanas, prevention of MBD appears to require a sufficient dose of UV-B radiation. The energy of UV-B radiation is necessary to fracture a bond in the sterol ring structure of 7-dehydrocholesterol, a compound found in the skin of many animals, including basking lizards. 62,63 The product so formed, termed previtamin D, undergoes a temperature-dependent conversion to cholecalciferol or vitamin D₃. Vitamin D then circulates to the liver, where it is converted to calcidiol, which is the predominant circulating metabolite. As needed, calcidiol is metabolized further to calcitriol in the kidney. This is the active form that binds to nuclear binding sites and serves as a hormonal regulator of the synthesis of essential proteins, including the calcium-binding protein needed for the uptake of calcium by the intestines. In the absence of vitamin D metabolites, dietary calcium cannot be efficiently absorbed, leading to calcium deficiency and metabolic bone disease. In most animals the skin-derived supply of vitamin D can be replaced by dietary vitamin D, but this does not appear to be the case in the green iguana and some other basking lizards.21

The opportunity for thermoregulation within a defined thermal gradient may be important since the conversion of previtamin D to vitamin D is temperature-dependent. The most effective means of providing adequate UV-B exposure is the use of enclosures that permit some outside access to direct sunlight. Staff at some major zoos in temperate regions rotate iguanas and other large basking lizards to outdoor cages during the summer months, and hope that the vitamin D synthesized is sufficient to last through the winter months when the lizards are housed indoors. Iguanas in outdoor cages should have access to shade and shelter to allow them to self-regulate solar exposure and prevent overheating.

All sunlight is not equivalent. The atmosphere absorbs most UV-B below 290 nm before it reaches the earth's surface, and even higher wavelengths are substantially attenuated when the light path is long, as when the sun is low in the sky. As a consequence there are substantial latitudinal and diurnal varia-

tions in the UV-B irradiation of the earth's surface, with greater UV-B irradiation at midday, closer to the equator and in midsummer. 52,64 Thus, even if it were possible to design open, heated enclosures suitable for winter use by iguanas, the UV-B benefit would be minimal.

In some instances exposure of captive lizards to direct natural sunlight is not possible. Although window glass and many plastic materials filter out UV-B, it is possible to use a UV-B-transmitting plastic, such as Solacryl™ UVT (Polycast Technology Co., Stamford, CT) in skylight frames. It is critical to verify that skylight materials transmit UV-B and not just UV-A, the longer wavelength band of ultraviolet light that does not support vitamin D synthesis. While such materials gradually lose their ability to transmit UV-B, the effective life is measured in years rather than months. At the San Diego Zoo, changes in transmission of UV-B (at 295 and 300 nm) through a 0.25-inch-thick, earlier version of a Polycast product (New Polycast SUVT) were measured initially and were found to transmit light at 74 and 81%, respectively. Two years later transmission was found to be 52 and 59%, respectively. 60 Quantitative data on longer term diminution in light transmission are not available. Skylight placement relative to compass direction and basking sites is probably also important, although there is little information on vitamin D status of iguanas in cages with skylights.

Many zoos and hobbyists may have difficulty in providing iguanas exposure to direct sun or sun filtered through UV-B-transmissible skylights. The alternative is to provide UV-B by an artificial light source. Household incandescent bulbs do not emit UV-B and are thus not useful in this regard, and many fluorescent bulbs are also weak UV emitters. 65 Bernard²⁰ compared UV-B irradiation at a fixed distance (24 in or 61 cm) from 20 different fluorescent bulbs, and concluded that most commercial bulbs have such weak emission that they must be very close to animals to be of any value. Blacklights have high emission of UV-A but most have no more UV-B than daylight fluorescent bulbs. One tested blacklight (Sylvania 350 BL) was higher in UV-B than other bulbs that are commercially available, and may be useful if combined with a daylight fluorescent bulb such as the GE Chroma-50. It is critical that the radiation from these bulbs pass unfiltered to the animals; intervening glass panes will block UV-B. The lamp fixtures must also be set close to the basking sites of the iguanas if the amount of energy reaching the skin is to be sufficient to permit vitamin D synthesis. For example, the basking sites of the green iguanas in our study of three different fluorescent bulbs (see Figure 4.7) were 15 cm from the bulbs, which remained on 12 hours per day. It is unlikely that the circulating calcidiol levels would have been as high if the animals had been much farther from the bulbs.

We have subsequently maintained green iguanas for more than 10 years and juvenile Komodo dragons for more than 5 years under either GE Chroma 50 bulbs or a combination of GE Chroma 50 (or Sylvania 50) and GE BL 40 (black light) (General Electric Lighting, Cleveland, OH) lamps. All of these bulbs are weak UVB emitters^{20,60} but by installing them sufficiently close (no greater than 55 cm, 22 in, above cage floors and approximately 15-25 cm, 6-10 in, from the top basking branch) and keeping them illuminated 12 hours per day, animals have maintained circulating calcidiol concentrations that appear adequate and have been clinically normal (Allen, 1995, unpubl. data). Under these lighting conditions, metabolic bone disease has not reappeared in either iguanas or Komodo dragons.

In relation to a point source of light, the amount of incident energy on a surface declines in proportion to the inverse of the distance to the source squared. In other words, if the distance quadruples, the amount of incident energy will drop to about one-sixteenth. This creates a great problem in large naturalistic exhibits, since weakly emitting fluorescent lights may have no measurable impact on green iguanas at a distance of many feet. In such cases installment of UV-B-transmitting skylights may be the only option. At the National Zoological Park, green iguanas developed severe metabolic bone disease in the large Amazonia rainforest exhibit⁵⁴ because the installed windowpane material does not transmit UV-B (only UV-A), and the great size of the building made artificial lights ineffective. Despite their popularity, green iguanas are no longer kept in this exhibit.

The development of a more powerful yet safe artificial source of UV-B radiation is still underway. The exuberant claims of manufacturers who market bulbs specifically for use with basking reptiles should be treated with skepticism until it can be demonstrated in controlled studies that these bulbs have greater efficacy than normal fluorescent bulbs in promoting vitamin D synthesis in iguanas or other basking species. Bernard²⁰ found that an experimental bulb made specifically for her research by Sylvania (Sylvania Experimental Reptile Lamp) had a correlated color temperature and color rendering index similar to that of the sun. The lamp emitted 78.3 uW/cm² at a distance of 61 cm (24 in) with an energy distribution among UV-B. UV-A, and visible light of 9.0%, 25.6%, and 65.4%, respectively. Vitamin D synthesis in iguanas was supported, and an exposure time of 8 hours at 61 cm (24 in) was safe, based on standards set by the National Institute for Occupational Safety and Health.⁶⁰ Unfortunately, this bulb is still not available commercially.

One intriguing possibility for large exhibits is the establishment of preferred basking sites by strategic use of heat sources, and then placement of UV-B-emitting fluorescent bulbs in the immediate vicinity. The success of this strategy will depend on the amount of time green iguanas spend at these specific sites.

Many studies have demonstrated a positive response after lizards are exposed to artificial UV-B sources. However some iguanine lizards appear to circulate higher concentrations of 25 hydroxy vitamin D after exposure to natural sunlight⁶⁶. In this recent report the authors found that increases in 25 hydroxy D were significantly greater after lizards were housed in natural sunlight compared with those exposed to artificial lamps alone. The differences could obviously be due to the lower intenstiy of the lamps as compared with the energy provided by UV-B from the sun.

OTHER NUTRIENTS OF CONCERN

Amino Acids

The microbial populations found in the ruminant stomach are able to synthesize amino acids and some B vitamins which are passed to the intestinal tract.⁴⁰ Since most absorption of these micronutrients occurs in the small intestine it is unnecessary to provide dietary sources of these nutrients to ruminants. However, in the green iguana and other animals that ferment plant fiber in the hindgut (colon and cecum), the amino acids and vitamins are synthesized at a site distal to absorption sites, and it is unlikely that these contribute much to the nutrition of the host animal. Thus, nutritionists typically add amino acids and B vitamins to formulated diets for such species. A special case may exist with hatchlings that ingest adult feces, thus having an opportunity to utilize amino acids and vitamins of microbial origin.⁶⁷

Amino acids are the building blocks of protein. Animals require specific amino acids in fixed proportions to one another. In those domestic animals studied, 10-11 amino acids are considered essential, although many nonessential amino acids have been identified. 41 Amino acids of practical importance in the diets of herbivores, because of their low concentrations in many feed ingredients, include lysine, methionine plus cystine, and tryptophan. In the absence of any data on the requirements of iguanas, we have opted to use poultry estimates expressed as a percentage of dietary protein.68 The amino acid requirements of poultry have been extensively studied. Some amino acids can partially substitute for others so that recommended dietary levels may include sums of two amino acids, such as methionine plus cystine, or phenylalanine plus tyrosine.

When iguanas are fed protein in excess of need, when amino acids are not balanced with respect to need, or when dietary energy is insufficient for maintenance (causing tissue proteins to be catabolized for energy), the amino acids are deaminated and most of the nitrogen is incorporated into uric acid prior to excretion. Part of the carbon skeleton of uric acid is derived from the amino acid glycine. During rapid growth in poultry glycine synthesis may not keep up with the combined demand for protein synthesis and uric acid synthesis with the result that the birds may benefit from a dietary source of glycine, which is otherwise nonessential. 68,69 Whether iguanas ever grow quickly enough to require dietary glycine is not known. Since the amino acid serine can substitute for glycine, the recommendation to include glycine in diets is usually expressed as the sum of glycine and serine.

Thiamin or Vitamin B₁

Thiamin, or vitamin B₁, is an essential nutrient for monogastric herbivores. In appropriately fed ruminants, microbes in the rumen synthesize sufficient amounts of thiamin to satisfy the host animal's needs. Thiamin functions in key energy-generating reactions and in nerve transmission. 70 Deficiency signs are usually observed in reptiles fed dead fish, as some fish species contain enzymes, thiaminases, which destroy thiamin in postmortem tissues. Many foods are poor sources of this vitamin, but the germ of cereal grains are a good thiamin source. Thiamin deficiency should not be seen in green iguanas fed a diet consisting of mixed greens and a manufactured feed that has supplemental thiamin added. The coccidiostat, amprolium, is commonly used at low levels to inhibit bacterial thiamin transport. If amprolium is fed at higher levels chicks exhibit signs of thiamin deficiency and poor growth. 70 Compared to mammals, poultry appear to develop neuromuscular signs associated with thiamin deficiency relatively rapidly. Polyneuritis in chickens occurred only after 3 weeks of feeding a thiamindeficient diet. 69 Ataxia, muscle spasms, and paralysis are common signs in chicks and adult birds. Opisthotonos, a retraction of the head, is a result of anterior neck muscle paralysis. Thiamin is relatively stable and frozen foods do not lose appreciable amounts. Since it is a water soluble nutrient, much thiamin may be lost in the drip produced by thawing moist foods.

Dehydrated fruits treated with sulfites also have significant losses of thiamin.

Vitamin A

Vitamin A, or retinol, is a fat-soluble nutrient essential to maintenance of the integrity of epithelial cells and for production of visual pigments necessary for sight. Beta carotene and some other carotenoid pigments in plants can serve as precursors of vitamin A in herbivorous mammals and presumably also in herbivorous reptiles. By contrast, the domestic cat lacks an enzyme that cleaves beta-carotene to form retinol and thus must receive a dietary source of retinol.41 Clinical and pathologic signs resembling vitamin A deficiency have been noted in reptiles, and especially in young turtles fed dried insects.^{2,45} Signs associated with suspected hypovitaminosis Ainclude squamous metaplasia and keratinization in the pancreas, kidney, and urinary bladder. Lesions of the eye are particularly characteristic signs in laboratory animals, and apparently in turtles.45 Although the vitamin A requirements of reptiles have not been studied, the high concentrations of carotenoids in leafy greens make a deficiency unlikely when a salad-type diet is fed, and vitamin A is invariably added to commercial diets. However, because vitamin A is toxic in relatively modest amounts, vitamin A toxicosis should be suspected when diets are over supplemented with vitamin preparations (see section on supplements).

Vitamin C

The ability of animals to synthesize vitamin C (ascorbic acid) varies greatly among vertebrates. Many mammals possess L-gulonolactone oxidase (GLO), the enzyme necessary for the production of ascorbic acid, but anthropoid primates, many bats, and the guinea pig do not. Of the reptiles studied, 11 species were found to have renal synthesis of ascorbic acid, via GLO, although the green iguana was not examined. 71 Although it is sometimes speculated that mouth rot in snakes and lizards is due to vitamin C deficiency, 45 this has not been verified. Vosburgh et al.72 found that when vitamin C was included in a diet fed to garter snakes their synthesis of vitamin C declined, but ascorbic acid levels in tissues were not changed. In a preliminary study of green iguanas, we noted a modest growth response to the addition of vitamin C to the diets of hatchlings (Oftedal and Allen, 1987, unpubl. data), but no deficiency signs were noted in those without supplemental C. It is possible that the growth response was due to other effects of

vitamin C, such as improved absorption of inorganic iron. In willow ptarmigan (Lagopus lagopus), very young chicks require a dietary source of ascorbic acid since they are not able to synthesize it at a high enough rate to meet tissue needs, whereas older birds synthesize sufficient amounts and do not require a dietary source of vitamin C.73 Since it is not known if hatchling or adult green iguanas can synthesize vitamin C, diets should contain a source of this nutrient. Fresh greens are usually good sources of vitamin C and tend to be higher in vitamin C than most fruits.74 If greens are consumed as part of the diet of green iguanas vitamin C intake should be sufficient. Some commercial iguana diets also include vitamin C; check the label for ascorbic acid or ascorbate as an ingredient.

Vitamin E

In reptiles, vitamin E deficiency most commonly occurs in carnivorous species that are fed fish from which much of the vitamin E has been lost due to oxidation.⁷⁵ For example, steatitis in alligators has been attributed to vitamin E deficiency. 76 Vitamin E deficiency has not been well documented in green iguanas, although Farnsworth et al.77 reported improvement in a green iguana treated with a vitamin E and selenium preparation. The animal presented with a history of lethargy, depressed appetite, rigid flexion of the carpal joints, spasmodic contractions and fasciculations of the limbs, and apparent muscle weakness, but was radiographically normal and did not respond to IP calcium gluconate or oral calcium supplementation. One unusual dietary feature of this iguana was the inclusion of a commercial mink food which may have been high in polyunsaturated fish oils that easily become rancid, with loss of vitamin E activity. After injection with sodium selenate and alpha-tocopheryl acetate, the clinical signs regressed to normal. Such a case history is more suggestive than definitive, as neither muscle histology, dietary vitamin E intake, nor circulating vitamin E (alpha-tocopherol) levels were examined.

Unfortunately, circulating levels of alpha-tocopherol may have limited diagnostic value because of the lack of substantiated normal values for green iguanas, the large range of normal values among species (from <0.5 to 30 µg/ml),⁷⁸ the relatively large variation among samples collected at short intervals (e.g., a coefficient of variation of 17% among samples taken at 3-hour intervals over 72 hours in horses⁷⁹), and the preferential release from stores.80

However, there is some evidence that circulating levels in iguanas respond to dietary intake. In an

attempt to evaluate different forms of vitamin E as dietary ingredients, Pappas et al.81 monitored circulating alpha-tocopherol in several mammalian herbivores and in green iguanas. Iguanas were fed diets containing 441 mg/kg of dl-alpha-tocopheryl acetate, the most commonly used dietary form, or equimolar amounts of d-alpha-tocophervl acetate, d-alphatocopherol, or d-alpha-tocopheryl polyethylene glycol 1000 (TPGS), a water soluble form of the vitamin. Serum alpha-tocopherol in the iguanas was measured after 21 days and again at 82 days. Iguanas fed dalpha-tocopherol or d-alpha-tocopheryl acetate had higher alpha-tocopherol levels in blood (approximately 16 and 17 µg/ml serum) at 82 days as compared to baseline and to dl-alpha-tocopheryl acetate or to TPGS at 82 days. As normal values are not known, this increase may or may not have health implications. The iguanas that were fed dl-alpha-tocopheryl acetate, the commonly used supplemental form of vitamin E in formulated feeds for domestic animals, had circulating levels of alpha-tocopherol of 12 µg/ml.

With the recognition that nondomestic animals may have higher vitamin E requirements than domestic animals,4 we recommend including a relatively high level of vitamin E (150 IU/kg) in iguana diets. One IU is equivalent to 1 mg of dl-alphatocopheryl acetate or 0.67 mg d-alpha-tocopherol. Many fresh greens have moderate concentrations of alpha-tocopherol, ranging from 3 in lettuce (variety not stated) to 25 in spinach (mg/kg FWB). 78 A feeding program that combines an appropriate manufactured feed and moderate amounts of greens should be adequate to meet vitamin E requirements of the green iguana.

Minerals Required in Trace Amounts

A number of trace elements are required by birds and mammals for a variety of functions, including as components of enzymes, hormones, or other metabolically active proteins (e.g., iron in hemoglobin, copper in ceruloplasmin, manganese in pyruvate carboxylase, zinc in alkaline phosphatase, iodine in thyroxine, and selenium in glutathione peroxidase). 82,83 It is thus certain that they are also required by reptiles such as the green iguana, and it is likely that the amounts required (as ppm or mg per kg diet) are similar to studied birds and mammals. Type of diet may be as important as the species being fed in determining an appropriate dietary level, since a number of factors in feed ingredients can reduce (e.g., phytate, oxalate, and calcium) or enhance (e.g., vitamin C) trace element absorption from the digestive system.

We recommend that trace elements be included in diets at a level that would meet the highest reported requirement of other vertebrates. For example, we consider 70 ppm manganese to be appropriate for iguana diets since species of poultry are known to require 60-70 ppm during growth, even though cattle, sheep, and horses require 30-40 ppm and omnivorous and carnivorous mammals even less. 41,65 Copper is particularly problematic because of its toxicity even at relatively low levels in some species. For example, sheep require about 10 ppm dietary copper (or even higher if dietary molybdenum is elevated) but can develop chronic copper toxicosis involving increasing tissue copper followed by a hemolytic crisis when ingesting diets with as little as 30-40 ppm. 82,84,85 Great caution should be exercised when using vitamin-mineral supplements containing copper not to exceed appropriate use rates (see below).

Water

Water may be a critical need for iguanas maintained on dry diets. Some iguanas may not drink standing water unless trained to do so. Others appear to relish a large dish of water and may soak themselves and drink. For animals that do not drink free water, particularly those on dry diets, misting the iguana and cage "furniture" once or twice daily is recommended to raise humidity. Iguanas may also lap water droplets from surfaces.

RECOMMENDED NUTRIENT LEVELS FOR IGUANA DIETS

In formulating a nutritionally complete feed it is necessary to establish target nutrient levels that will meet the estimated nutrient requirements of iguanas and include a sufficient safety margin to compensate for poor utilization of some nutrients as well as nutrient losses that occur during the manufacture and storage of the diet. As the nutrient requirements of reptiles and other nondomestic animals are mostly estimated by comparison to better-studied domestic animals, 41 a further safety margin representing possible interspecies differences needs to be incorporated. Thus a well-designed iguana diet will invariably be higher in a number of nutrients than are diets for domestic animals such as rabbits, horses, or dogs, even though the underlying process of formulating and manufacturing such diets is similar.

The levels of nutrients that we recommend for iguana diets are listed in Table 4.2. For most nutri-

Table 4.2 Recommended nutrient levels¹ for green iguana diets.

Nutrient	Dietary Level (%	or per kg feed)	Daily Amount (per kg BM)		
Amino acids ²		_			
Arginine	1.4	%	98	mg	
Glycine + 5erine	0.9	%	63	mg	
Histidine	0.5	%	35	mg	
Isoleucine	1.0	%	70	mg	
Leucine	1.75	%	123	mg	
Lysine	1.4	%	98	mg	
Methionine	0.45	%	32	mg	
Methionine + Cystine	0.95	%	67	mg	
Phenylalanine	0.9	%	63	mg	
Phenylalanine + Tyrosine	1.6	%	112	mg	
Threonine	0.95	%	67	mg	
Tryptophan	0.24	%	17	mg	
Valine	1.2	%	84	mg	
Linoleic acid	1.0	%	84	mg	
Crude fiber	6–10	%	42	mg	
Acid detergent fiber	10–18	%	70	mg	
		general season (Season)			
Calcium	1.1	%	77	mg	
Phosphorus	0.6	%	42	mg	
Potassium	0.5	%	35	mg	
Sodium	0.2	%	14	mg	
Magnesium	0.15	%	11	mg	
Iron	100	mg	0.7	mg	
Copper	10	mg	0.07	mg	
Manganese	70	mg	0.49	mg	
Zinc	80	mg	0.56	mg	
lodine	0.6	mg	0.004	mg	
Selenium	0.3	mg	0.002	mg	
Vitamins as 1 - 20 10 2 military	gradien de la		with with a section as a second	4.00	
Vitamin A	8,000	IU	56	IU	
Vitamin D ³					
Vitamin E	150	IU	1.1	IU	
Vitamin K	2	mg	0.14	ΙU	
Vitamin C ⁴	200	mg	1400	μg	
Thiamin	5	mg	35	μg	
Riboflavin	5	mg	35	μg	
Pantothenic acid	25	mg	175	μg	
			continued on the	next page	

Table 4.2 (continued)

Nutrient	Dietary Level	(% or per kg feed)	Daily Amount (per kg BM)		
Niacin	90	mg	630	μg	
Pyridoxine (B ₆)	6	mg	42	μд	
Folic acid	0.8	mg	5.6	μд	
Biotin	0.25	mg	1.8	μд	
Vitamin B ₁₂	25	μg	0.18	μд	
Choline	1200	mg	8400	μд	

¹Expressed on a dry matter basis.

²The recommended protein and amino acid levels have been demonstrated to support high growth rates and good health of hatchling and young (<6 months) juveniles; for subadults, protein levels of 22% may be adequate, and for nonreproductive adults protein levels of 15–17% may suffice. For lower protein diets, amino acid levels should be adjusted to maintain the same ratio to dietary protein as in the 26% protein diet.

 3 No dietary level of vitamins D_{2} or D_{3} has been shown to prevent vitamin D deficiency and hence iguanas should always be provided with ultraviolet-B radiation to permit vitamin D synthesis (see text).

⁴Vitamin C may be provided by provision of leafy greens.

Abbreviations: IU = International Units, kg = kilogram, mg = milligram, µg = microgram.

ents actual requirements will be lower, so a diet containing lower levels will not necessarily produce nutritional deficiency but since precise requirements are not known use of lower levels entails greater risk. We have developed these target levels by comparison to known requirements for domestic mammals and birds, as well as based on experience in formulating diets for a wide variety of zoo animals. Diets made according to these specifications have been used for many years with iguanas without evident nutritional problems other than metabolic bone disease attributable to lack of ultraviolet light and correctable by provision of artificial sources of UV-B radiation. We do not include a recommended level of vitamin D₃ since we are unaware of any dietary level of this nutrient that has been demonstrated to prevent vitamin D deficiency and yet be safe for long-term feeding. Recognizing that older iguanas do not likely need as much protein as hatchlings, we have included two intermediate levels: 1) \geq 22% for subadults and 2) 15–17% for nonreproductive adults. The amino acid levels can be reduced to a corresponding degree, maintaining the ratio of amino acid: protein for each amino acid.

Baer et al.²³ demonstrated that food intake in iguanas was proportional to body weight, with an average dry matter intake of about 0.7% of body mass per day, regardless of dietary fiber content. Assuming a daily dry matter intake of 7 g per kg body mass (BM), the recommended dietary levels can be converted to recommended daily amounts per kg BM (see Table 4.2) which is useful in determining appropriate rates at which to use vitamin and mineral supplements (see below).

The recommended dietary levels in Table 4.2 can be used as benchmarks against which iguana diets can be compared. Unfortunately, neither the guaranteed analysis nor other label information on commercial diets are sufficient for evaluation, and laboratory analysis for such a broad range of nutrients is very costly. Diet manufacturers are usually unwilling to provide calculated or assayed levels of all nutrients, as they regard such information proprietary, but they may be willing to divulge information on specific nutrient levels upon request or to assure that nutrient levels meet or exceed those listed in Table 4.2.

We are aware of two diets that are commercially available that meet these standards (Table 4.3), although they are not sold through pet shops. Institutions such as zoos can purchase these products directly from the manufacturers: Zeigler Bros., Gardners, PA and Marion Zoological, Plymouth MN. Herpetological associations may also be able to buy in bulk for their members.

Of the 31 pet store diets that we purchased and assayed for major constituents and major minerals, two met the nutrient standards of Table 4.2 with regard to those nutrients assayed (see Table 4.3), and an additional five met the lower protein standard for subadults. However, there is no certainty that levels of vitamins or trace minerals are appropriate in all of these diets. In general, large, reputable companies that employ nutritionists are likely to manufacture a nutritionally balanced diet, whereas very small businesses may or may not have access to the expertise to produce nutritionally balanced products. If there is a question about a specific product, we ad-

Table 4.3 Commercial diets that meet nutrient recommendations.

Diets that, by calculation and/or analysis, meet recommendations for juvenile or subadult iguanas for major constituents, amino acids, minerals, and vitamins:1

Zeigler Iguana Diet, NZP Version 7 (25% CP), Zeigler Bros., Gardners, PA. Marion Reptile Food for herbivorous reptiles, Marion Zoological, Inc., Plymouth, MN

Diets that, by analysis, meet recommendations for juvenile iguanas for major constituents and major minerals:² Zoo Med Juvenile Formula Iguana Food, Zoo Med, San Luis Obispo, CA Five Star Iguana Diet, Five Star Reptile Foods, Riverview, FL

Diets that, by analysis, meet recommendations for subadult iguanas for major constituents and major minerals:3 Zeigler/Farnam Iguana Diet, Zeigler Bros., Gardners, PA

Reed's Iguana and Tortoise Food, Tetra Terrafauna, Morris Plains NJ

Reed's Iguana and Tortoise Food, Juvenile, Tetra Terrafauna, Morris Plains, NJ

Mill Creek All Natural Iguana Food, Mill Creek Farms

Nutri-Grow Herbisaur, American Reptile Inc., Dry Ridge, KY

¹Recommended nutrient levels as in Table 4.2.

 2 Nutrient concentrations (DMB) as follows: protein ≥26%, fat ≥3%, acid-detergent fiber 10–18%, calcium ≥1.1%, phosphorus ≥0.6%, Ca:P ratio 1.0-3.0.

³Nutrient concentrations (DMB) as follows: protein 22-26%, fat ≥3%, acid-detergent fiber 10-18%, calcium ≥1.1%, phosphorus ≥0.6%, Ca:P ratio 1.0-3.0.

vise contacting the company and asking to speak to the nutritionist who developed the product. This should be a person with an advanced degree in animal nutrition or feed manufacturing, and with prior experience in diet formulation.

USE OF PRODUCE

Although research has shown that iguanas will breed successfully, grow well, and live for many years on nutritionally balanced manufactured diets, there is a natural tendency of hobbyists and zoo keepers to want to feed produce. Produce is often palatable to iguanas, and may be helpful in inducing them to eat commercial products. For example, moist leafy greens can be coated with a meal-type diet or ground up pellets to accustom them to these products. Feeding palatable foods also has the advantage that animals may come to the front of the cage where they be more carefully observed for any evidence of injury, disease, weight loss, etc. Produce can also be a valuable source of vitamin C and other labile vitamins that may deteriorate in a manufactured feed during storage. High-moisture produce may be an important water source for animals fed dry diets.

Excessive use of produce may lead to nutrient imbalances, however. Salad-type diets that have been commonly used for iguanas and other herbivorous

reptiles are typically low in protein, calcium, trace minerals and some vitamins (Tables 4.4, 4.5). Two of the diets (A and B) included in Table 4.4 included eggs, dog food, feline diet, and/or rabbit diet in an attempt to address low protein and mineral levels, but they also contained fruits and tubers, which are low in these nutrients. Largely due to the inclusion of a vitamin/mineral supplement at about 1% of the diet (as-fed basis), diet B had higher levels of many micronutrients as compared to unsupplemented diet A. The composition of the supplement is critical to the overall composition of the offered diet. In the case of diet B, the supplement Pervinal improved the levels of many nutrients such as calcium, phosphorus, sodium, copper, niacin, and vitamins A and B₁₂; yet other nutritional imbalances were not corrected (see Table 4.5). Diet C is a hypothetical diet representing a mix of leafy material with flower buds (broccoli), immature seed pods (green beans), and a nonstarchy tuber (carrots), but without sweet fruits, animal products, or supplements. Although this diet is more balanced than diets A and B, it is still marginal in calcium and low in some trace elements and vitamins. The lack of preformed vitamin A may not be a problem as the green iguana can probably convert abundant beta-carotene and perhaps some other carotenoids into vitamin A as do other herbivores.

Animals in captivity are invariably fed a much narrower range of plants than they ingest in the wild

Table 4.4 Salad-type diets fed to herbivorous reptiles at two major US zoos in the 1980s (Diets A and B) and hypothetical salad-type diet based largely on greens (Diet C).

	Amount			
Food Item	Diet A	Diet B	Diet C	
1. Leafy greens	Markey	in a ria	10.1	
Spinach	91.2	and the		
Enclive Kale	afiiki n⊥L	4000	150 100	
Lettuce, romaine	# <u>1</u>		200	
Swiss chard	ويوا	Marie Per a l ia, i	+150	
2. Other vegetables				
Broccoli			150	
Beans, green	65.7	184.0	150	
Carrot		103.9	100	
Sweet potato	27.5	190.0		
3. Fruit				
Apple	29.0	138.5		
Banana ,	6:0	56,8		
Grape :	77.7	5. 3— 7%		
Orange .'	_{ு.} 81.3	86.6		
4. Other items	y-reg-range ra			
Egg, whole, cooked	36.3	28.3	_	
Canned dog food	_	11.0	_	
Rabbit chow	5.5	_	_	
Frozen feline diet	18.1			
Pervinal		10.9		
Total	1000	1000	1000	

(see Baer, Chapter 3), and it is common for a few types of produce to predominate, such as lettuce, kale, cabbage, spinach, carrots, or apples. While modest quantities of any particular type of produce may not be harmful, a preponderance of one or a few plant materials increases the likelihood of nutritional imbalance and unintended physiologic effects. For example, spinach, rhubarb, beet greens, prickly pear, and some garden weeds such as sorrel (Oxalis spp.), dock (Rumex spp.), and purslane (Portulaca oleracea), contain high levels of oxalic acid salts (oxalates).86,87 In humans and studied animals, high intakes of oxalate (2-30 g) cause a local corrosive effect, followed by systemic effects involving cardiovascular, neuromuscular, and nervous systems, and finally renal impairment. Oxalates may reduce the intestinal absorption of calcium, cause a drop in circulating calcium levels and precipitate as crystals in the kidneys. Excessive oxalate intakes from forages can be lethal, although there appear to be differences

among species in their susceptibility to oxalate poisoning. 86,87

Most vegetables consumed in western countries have low to moderate levels of oxalates and many supply some calcium. The effect of high-oxalate, lowcalcium diets on green iguanas is not known. Given that problems associated with calcium homeostasis are widely reported in iguanas, we recommend that foods such as spinach, rhubarb, and parsley which contain significant amounts of oxalate (97-780 mg/ 100 g, FWB) should be avoided. Intermediate oxalate levels occur in runner beans (7-62 mg/100g), carrots (7–23 mg/100g), and celery (13–18 mg/100 g, FWB).87 Since ascorbic acid is a precursor of oxalic acid in some animals and in humans, oxalate stone formation has been attributed to excessive dietary supplementation with ascorbic acid. Although healthy humans can tolerate up to 10 g of ascorbic acid per day. patients with renal insufficiency are advised to restrict vitamin C intake to 100-200 mg/day. The effects of high dietary vitamin C levels in the green iguana have not been studied.

We conclude that oxalate-rich foods should be used in moderation. The same warning applies to plants that are rich in glucosinilates, including many plants in the family Brassicaceae, such as kale, cabbage, brussel sprouts, Swiss chard, kohlrabi, rutabaga. broccoli, and radishes. In humans, rabbits, livestock, and other mammals, high intakes of glucosinilates can result in the enlargement of the thyroid (goiter) and impairment of its function.86,89 Hypothyroidism has been reported in tortoises^{2,90} with the suggestion that ingestion of goitrogenic plants may have contributed. Wallach and Hoff 45 reported an iguana, Cyclura cornuta, with a thyroid gland 20 times the size of that in a normal animal, but dietary information was not provided. Whether a goitrogenic effect occurs in green iguanas is not known, but warrants study. While plant materials such as kale, cabbage, and broccoli are routinely included in iguana diets without adverse effects, these should not be the sole produce items used.

We recommend that produce used in iguana diets be limited to leafy greens and nonstarchy vegetables as in diet C; fruits are best avoided. A variety of items is more likely to counteract the nutritional deficits or imbalances in any particular item, and may enhance the interest of iguanas in their food. For example, iguanas are partial to fresh dandelion and hibiscus flowers and may be attracted to colors. In general, produce should represent no more than 50% of the diet, on a fresh weight basis, with the remainder being one or more rationally formulated commercial diets.

Table 4.5 Calculated nutrient concentrations in salad-type diets listed in Table 4.4 as compared to recommended nutrient levels from Table 4.2.1

Selected Nutrients	Diet A	Diet B	Diet C	Respective % of Recommendation for Juvenile Iguana
Crude protein, %	10.4	12.3	25.7	47 - 56 - 96
Crude fiber, %	4.1	4.8	11.2	68 - 80 - 187
Calcium, %		0.6	0.9	27 - 55 - 82
Phosphorus, %	0.2	0.5	0.6	33 - 83 - 100
Sodium, %	0.11	. 0.26	0.46	55 - 130 - 230
Magnesium, %	0.14	0.18	0.19	93 - 120 - 127
Iron, ppm 📖 🚟 🚎	ja. 21.75	128		
Copper, ppm	6	10	>24	40 - 67 - >160
Zinc, ppm	55.17 24 - 5	27	511 of 1977	30 - 34 - >14
Manganese, ppm	15	13	>10	21 - 19 - 15
Vitamin A, IU/kg] (- 1592) ()	31,100	27	20 - 388 - 0
Vitamin E, IU/kg	>64	105	>30	>42 - 70 - >20
Vitamin C, ppm 📲 🤲	·····································	1978	4945	52 - 990 - 2473
Thiamin, ppm	3	11	8	60 - 220 - 160
Riboflavin, ppm	· * * 5	19	14	10 0 - 380 - 280
Pantothenate, ppm	15	32	37	60 - 130 - 150
Niacin, ppm	20	106	82	22 - 118 - 91
Folic acid, ppm	1.75	1.75	6.79	220 - 220 - 850
Vitamin B ₁₂ , ppb	2.5	27	??	10 - 108 - 0

ARE VITAMIN AND MINERAL SUPPLEMENTS BENEFICIAL?

Nutritional supplements should be necessary only if the vitamin and trace mineral concentrations in the commercial diets being fed are unknown or if such products are used more than 6 months after the date of manufacture, since substantial vitamin losses can occur. However, in such cases it is critical that the appropriate amount of supplement is used. Overuse of supplements is a major problem, since many people erroneously assume that a little more of a good thing won't hurt. Excesses of vitamin A, vitamin D, calcium, phosphorus, copper, and other trace minerals can produce toxicosis or unintended adverse effects on other nutrients. Unfortunately, most manufacturers of supplements for reptiles simply suggest that their supplements be sprinkled on food, without giving recommended dosages. This invites abuse.

A reasonable approach would be to define the nu-

trients of concern as those that are easily lost during the manufacture and storage of diets (e.g., vitamins A, B₆, B₁₂, C, and thiamin) and those that may be deficient in produce and/or in feeds (e.g., trace minerals), and to provide a proportion of daily requirements for these through a supplement. As a general rule supplements should be used only as a safety net and not as a replacement for a balanced diet based on a formulated feed and greens. However, the amount of supplement added must be measured accurately if the risk of unintended poisoning is to be minimized. The appropriate amount will depend on the nutrient concentrations in the supplement.

Very large differences in the nutrient concentrations in commercial vitamin-mineral supplements are evident in Table 4.6, in which nutrient amounts are presented per gram (g) of supplement. The rather different numbers provided by Donoghue and Langenberg⁹¹ for some of the same supplements may reflect calculation error. Values calculated from information on product labels and inserts are only as accurate as

Table 4.6 Nutrient amounts in several commercial vitamin and mineral supplements, expressed per g supplement.¹

Supplement:	Pervinal	Vionate	Centrum	ProBalance Canine	Formula VMA	Herptivite	Reptivite
Form:	powder	powder	tablets	powder	powder	powder	powder
Minerals			::> t '/1::'				#12 % /
Calcium, mg	45.4	104	108	13	18	44	211
Phosphorus, mg	42	48	83	10	14	22	106
Potassium, mg	20.8		27	19	3.5	3.3	18
Sodium, mg	16.8	10		_		1.1	16
Magnesium, mg	2.9	0.42	67	0.12	3.5	0.2	2.6
Iron, mg	0.72	0.55	10	1.3	3.5	7.7	0.44
Copper, mg	0.11	0.055	1.3	0.12	_	0.33	0.44
Manganese, mg	0.07	0.076	1.7	0.054	3.5	0.66	0.08
Zinc, mg	0.11	_	10	1.9	3.5	0.66	0.44
lodine, mg	0.002	0.022	0.10	0.024	0.04	0.08	0.002
Selenium, mg	_	_	0.017	0.002	_		
Vitamins 🛴 🦠		ten er er er		Applications of the second	Pair III	建设数	er german
Vitamin A, IU	520	220	3340	198	2640	1470 ²	220
Vitamin D ₃ , IU	104	22	267	16	176	220	23
Vitamin E, IU	0.5	0.12	20	2.4	3.5	11	0.22
Vitamin K, mg		_	0.02	0.022	0.07	0.04	_
Vitamin C, mg		2.5	40	11	5.3	4.4	3.1
Thiamin, mg	0.13	0.039	1.0	0.064	1.8	1.8	0.17
Riboflavin, mg	0.27	0.079	1.1	0.14	1.8	1.1	0.27
	V.27	0.075	111				
Pantothenate, mg	0.1	0.11	6.7	0.64	1.8	0.66	1.9
				0.64 0.55	1.8 5.3		
Pantothenate, mg	0.1	0.11	6.7			0.66	1.9
Pantothenate, mg Niacin, mg	0.1	0.11 0.28	6.7 13	0.55	5.3	0.66 6.6	1.9 0.66
Pantothenate, mg Niacin, mg Vitamin B ₆ , mg	0.1 1.1 0.026	0.11 0.28 0.010	6.7 13 1.3	0.55 0.064	5.3 1.8	0.66 6.6 1.1	1.9 0.66 0.07
Pantothenate, mg Niacin, mg Vitamin B ₆ , mg Folic Acid, mg	0.1 1.1 0.026	0.11 0.28 0.010 0.002	6.7 13 1.3 0.27	0.55 0.064 0.008	5.3 1.8 4.2 ³	0.66 6.6 1.1 0.07	1.9 0.66 0.07 0.11
Pantothenate, mg Niacin, mg Vitamin B ₆ , mg Folic Acid, mg Siotin, µg	0.1 1.1 0.026 —	0.11 0.28 0.010 0.002	6.7 13 1.3 0.27 20	0.55 0.064 0.008 17	5.3 1.8 4.2 ³ 1.1	0.66 6.6 1.1 0.07 0.88	1.9 0.66 0.07 0.11 26

¹Data obtained from product labels for the following: Pervinal Nutritional Supplement, St. Aubrey, 8 in 1 Pet Products, Inc., Brentwood, NY; Vionate Vitamin Mineral Powder for Pets, ARC Laboratories, Atlanta, GA; Centrum tablets, Lederle, American Cyanamid Co., Pearl River, NY (1 tablet = 1.5 g); ProBalance Canine, Escondido, CA (1 scoop = 6.0 g); Formula VMA, Mardel Laboratories, Inc., Glendale Heights, IL; Herptivite, Rep Cal Research Labs, Los Gatos, CA; Reptivite, Zoo Med, San Luis Obispo, CA.

these sources. For example, label information for Formula VMA (Mardel Laboratories, Glendale Heights, IL) lists folic acid and vitamin B_{12} concentrations as 120 and 250 mg per ounce, which are improbably high; the correct units are probably micrograms per ounce. Even if these data are excluded, there is a 40-fold or greater range in concentrations of a number of nutrients, including magnesium, manganese, zinc, iodine, vitamin $E_{\rm c}$, thiamin, pantothenate, vitamin $E_{\rm c}$

folic acid, and vitamin B_{12} . The nearly 20-fold difference in vitamin A and the nearly 25-fold difference in copper are of particular concern as these nutrients can be toxic at relatively low levels. Indiscriminate substitution of one supplement for another could cause major changes in the composition of a diet.

How then does one determine how much to use? In our view, the greatest risk with supplement use in most animals is vitamin A toxicosis, both because of

²Supplied as betacarotene (0.88 mg/g); biological activity of 50% (as compared to retinol) assumed.

 $^{^3}$ Concentrations listed as 250 mg vitamin B $_{12}$ per ounce and 120 mg folic acid per ounce on label. This is likely an error in units which should read micrograms per ounce, such that per g concentrations would be 0.0042 mg/g folic acid and 8.8 μ g/g vitamin B $_{12}$.

the toxicity of retinol and related vitamin A compounds and because of the high levels that are often included in supplements. The National Research Council⁵⁸ concluded that the safe upper level for vitamin A in animal feeds was 15,000-25,000 IU/kg for several species of fish (trout and salmon), birds (growing chickens, turkeys, geese, and quail), and mammals (rabbits, horses, and growing swine), although higher levels are apparently tolerated by cattle, goats, sheep, and cats. Thus chronic intake of vitamin A levels much above 2-3 times the recommended dietary level of 8000 IU/kg (Table 4.2) could produce toxicosis in some vertebrates, and possibly in iguanas or other reptiles. The most characteristic signs of hypervitaminosis A in animals are skeletal malformation, spontaneous fractures and internal hemorrhage, but a variety of other signs may also be present, including fatty infiltration and impaired function of the liver and kidneys.⁵⁸ To minimize the risk of hypervitaminosis A we recommend that the amount of a vitamin-mineral supplement used should be restricted to that amount that will meet (but not exceed) the recommended level of vitamin A.

We have calculated the amounts of various supplements that will supply 56 IU of vitamin A, the recommended daily amount per kilogram body mass (see Table 4.2). The amount of supplement to be used for a 1-kg iguana varies from 16 to 560 mg (Table 4.7). The likelihood of oversupplementation is particularly great with products that are very high in vitamin A (>1100 IU/g) as the very minute amounts recommended (<50 mg per kg iguana) are impractical to measure. For example, a 1-kg iguana should receive only about 1/100 of a Centrum tablet which weighs about 1.5 g. For this reason, we do not recommend use of supplements with several thousand IU vitamin A per gram, such as Centrum and Formula VMA. Although the Herptivite has a calculated vitamin A activity of nearly 1500 IU/g, this is provided as beta-carotene, which is unlikely to produce toxicosis.

The benefit from a supplement will depend in part on the contributions of other nutrients when the maximal daily amount of supplement is used. In Table 4.7 the amounts of minerals and vitamins supplied by various supplements at this use rate are expressed as a percentage of the recommended daily amounts for these nutrients (as listed in Table 4.2). Since these supplement amounts were calculated to supply the recommended daily amount of vitamin A, the percentages for vitamin A are of course 100 for all supplements. We arbitrarily define a supplement as a "poor," good," or "excellent" source of a nutrient if it supplies <25%, 25–75%, and >75% of the recommended daily

amount (see Table 4.2) for that particular nutrient. On this basis Pervinal, Centrum, Formula VMA, and Herptivite are poor sources of macrominerals and many trace minerals although they are good or excellent sources of many vitamins. Vionate is a good source of calcium, phosphorus, and some vitamins but not of most trace minerals (except iodine) or vitamin E. ProBalance Canine and Reptivite are good or excellent sources of most nutrients although ProBalance Canine is a poor source of manganese and vitamin B_{12} , while Reptivite is a poor source of manganese and vitamin E. All of the supplements were poor sources of manganese. The high copper level of Reptivite is a matter of concern if this supplement is used in amounts much greater than 250 mg/kg per day.

Other supplements marketed for use with herbivorous reptiles include the following: vitamin supplements such as Nekton-Rep (Nekton USA, Clearwater, FL), Reptisol (Tetra Terrafauna, Morris Plains, NJ), and Biovite Plus (Ocean Nutrition Corp., San Diego, CA); calcium-phosphorus supplements with added vitamins such as Reptical (Tetra Terrafauna, Morris Plains, NJ), Reptovit (Tetra Terrafauna, Morris Plains, NJ), and 2:1 Calcium/Phosphorus Powdered Supplement with Vitamins (Ocean Nutrition Corp., San Diego, CA); and multimineral supplements such as Miner-All 0 (Sticky Tongue Farms, Menifee, CA). While some of these may have value in specific circumstances, we prefer supplements that have both labile vitamins and trace minerals, as these are the nutrients apt to be limiting in a diet based on a commercial feed and leafy greens. As with multiple vitamin and mineral supplements, the amounts used should be small to minimize the risk of vitamin A and copper toxicoses.

SUMMARY OF RECOMMENDATIONS

- 1) Diagnosis of a nutritional deficiency or toxicosis should include an evaluation of nutrient intakes in relation to estimated requirements or recommended levels.
- 2) With the advent of nutritionally balanced iguana feeds, it is no longer necessary or advisable to feed salad-type diets as these are often nutritionally imbalanced.
- 3) Dry formulated feeds have proven effective in rearing and breeding iguanas over many years and, if nutritionally complete, can be fed as the sole food.
- 4) The choice of a commercial iguana feed must be made carefully because various products differ

Table 4.7 Amount of supplement to supply the recommended daily amount of vitamin A for a 1-kg green iguana, and the percentages of recommended levels of other nutrients contained in this amount.¹

Supplement: Form:	Pervinal powder	Vionate powder	Centrum tablets	ProBalance Canine powder	Formula VMA powder	Herptivite powder	Reptivite powder
Amount (mg)	110	250	16	280	21	38	250
Minerals (%)					lawa ang paga ang pa		
Calcium	6	35	2	5	0.5	2	70
Phosphorus	11	29	3	7	0.7	2	64
Potassium	6		1	15	0.2	0.4	13
Sodium	13	19	_		_	0.3	30
Magnesium	3	1	11	0.3	0.7	0.1	6
Iron	11	20	29	52	11	42	16
Copper	17	20	31	47	_	18	160
Manganese	2	4	6	3	15	5	4
Zinc	2	_	31	95	13	5	20
lodine	5	133	40	161	18	70	13
Selenium			10	22		_	
Vitania (6):			1000	erlature : 1991, commi	der it branchs	emilia :	
Vitamin A	100	100	100	100	100	100	100
Vitamin E	5	3	31	63	7	40	5
Vitamin K		_	2	45			
Vitamin C		45	48	224	8	12	56
Thiamin	41	29	49	52	107	192	120
Riboflavin	82	57	54	113	107	120	200
Pantothenate	6	16	64	104	21	14	272
Niacin	19	11	35	25	18	40	27
Vitamin B ₆	7	6	52	43	89	100	41
Folic Acid		10	80	42	1600²	45	480
Biotin			19	269	1.3	2	384
Vitamin B ₁₂	25	22	39	216	107000 ²	168	973
Choline	8	17		32	0.9	4	_

¹Percentages are calculated as: Nutrient % = 100 · (nutrient amount in stated supplement amount)/(recommended daily nutrient amount per kg body mass) where the recommended daily amounts are those in Table 4.2.

greatly in nutrient composition and some appear to be nutritionally inadequate.

- 5) Because of their high protein requirement for growth, juvenile iguanas should be fed a diet containing about 26% protein on a DMB.
- 6) Feeding of a lower protein (about 15–17% DMB) diet is advisable for older iguanas susceptible to renal disease or afflicted by articular gout, but there is no convincing evidence that high protein diets predispose iguanas to gout.
- 7) Diets for juvenile green iguanas should contain a

- moderate amount of fiber (10–18% acid detergent fiber or 6–10% crude fiber), although adult iguanas may be able to tolerate somewhat higher levels.
- 8) Diets should contain at least 1.1% calcium and 0.6% phosphorus (DMB), and a Ca:P ratio of 1:1 to 3:1.
- 9) Exposure to ultraviolet-B (UV-B) light appears to be essential if iguanas are to maintain adequate circulating levels of vitamin D metabolites, and if they are to avoid vitamin D deficiency with consequent MBD and metastatic mineralization (extraskeletal calcification).

²These high values may reflect an error in labeling (see Table 4.6).

- 10) Midday sunlight is an excellent source of UV-B, but relatively few window materials permit UV-B transmission; due to atmospheric absorption of UV-B, solar exposure is likely ineffective in winter months in temperate zones.
- 11) An adequate amount of UV-B irradiation can be achieved using weakly-emitting fluorescent bulbs if these are placed close to the preferred basking sites and if daily exposure times are long (12 hours).
- 12) Reliance should not be placed on dietary vitamin D sources because dietary vitamin D appears to be ineffective in preventing MBD.
- 13) As soft tissue calcification can occur in vitamin D-deficient green iguanas, this finding is not in itself diagnostic of vitamin D toxicosis as is sometimes reported.
- 14) Specific concentrations of other vitamins and minerals are recommended for iguana diets based on both theoretical considerations and practical experience in feeding formulated diets to large numbers of iguanas; examples of diets that meet these recommendations are provided.
- 15) Produce can enhance diet palatability, provide a source of vitamin C and other vitamins, and be a source of water, but it should not be used in excess or nutritional imbalance may result.
- 16) Offered produce should be limited to a variety of leafy greens, flowers, and nonstarchy vegetables; fruit, starchy tubers and high-oxalate foods (such as spinach, rhubarb, and parsley) should be used sparingly, if at all.
- 17) Vitamin and mineral supplements should not be necessary if a well-balanced commercial diet is fed with modest amounts of produce.
- 18) If a supplement is used, the amount provided should be restricted to that amount that supplies the daily requirement for vitamin A, but at this level many supplements are poor sources of other vitamins or trace minerals.
- 19) If dry diets are used as a primary food, fresh water should be available at all times; iguanas that are reluctant to drink should be misted daily or soaked several times per week.

ACKNOWLEDGMENTS

We are especially indebted to Dagmar Werner who invited us to participate in iguana breeding and rearing efforts in Panama and Costa Rica, provided hatchling iguanas to the National Zoological Park, and made available funds from the Alton Jones Foundation to support initial studies. Research at the Na-

tional Zoological Park was also funded by the Smithsonian Scholarly Studies Program (Smithsonian Office of Fellowships and Grants) and the Friends of the National Zoo. The Departments of Animal Health and Pathology at the National Zoological Park were instrumental in recognizing and interpreting metabolic bone disease. We are grateful to the many individuals who devoted effort, ideas, and data to the green iguana project at the National Zoological Park, including the following: D. Baer and J. Bernard, who conducted thesis research; P. Barboza, A. Hunt, M. Jakubasz, L. Jayawickrama, W. Price, T. Tuchak, and L. Vilarin, who collected and/or assayed samples; R. Montali, D. Nichols, L. Richman, and Y. Schulman, who performed necropsies, evaluated tissues, and provided serum chemistry data; M. Bush, S. Citino, S. Murray, and L. Tell, who provided veterinary care and evaluated clinical signs; M. Deal, F. Kohn, K. Morrison, and M. Roberts, who were responsible for animal husbandry; and P. Barboza who helped oversee the project for several years. We thank T. Christopher for obtaining the samples of commercial feeds and vitamin-mineral supplements; and M. Subramanyam of Zeigler Bros. who assisted in diet formulation.

REFERENCES

- 1. Cayot LC and Oftedal OT: The importance of nutrition in rearing programs for Galapagos land iguanas and giant tortoises. Desert Tortoise Council Proc. 1995 Symposium, Las Vegas, 1996, pp 51-53.
- 2. Marcus LC: Veterinary Biology and Medicine of Captive Amphibians and Reptiles. Lea and Farber, Philadelphia, 1981.
- 3. Frye FL: Special medicine: amphibians and reptiles. Feeding and nutritional diseases, in Fowler ME (ed): Zoo and Wild Animal Medicine. WB Saunders Co., Philadelphia, 1986, pp 139-151.
- 4. Fowler ME: Metabolic bone disease, in Fowler ME (ed): Zoo and Wildlife Medicine. 2nd ed. WB Saunders Co., Philadelphia, 1986, pp 69–90.
- 5. Wright KM: Metabolic bone disease in reptiles. Reptile and Amphibian Magazine No. 2:60-68, 1993.
- 6. Burgmann PM, McFarlen J, and Thiesenhausen K: Causes of hypocalcemia and metabolic bone disease in Iguana iguana. J. Sm. Exot. Anim. Med. 2:63-68, 1993.
- 7. Oftedal OT and Allen ME: Nutrition and dietary evaluation in zoos, in Kleiman DG, Allen ME, Thompson KV, and Lumpkin S (eds): Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, 1996, pp 109-116.
- 8. Oftedal OT, Chen TC, and Schulkin J: Preliminary observations on the relationship of calcium ingestion to vitamin D status in the green iguana (*Iguana iguana*). Zoo Biol. 16:201-207, 1997.

- 9. Baer DJ: The nutrition of herbivorous reptiles, in Murphy JB, Adler K, and Collins JT (eds): Captive Management and Conservation of Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles, Ithaca, NY, 1994, pp 83–90.
- Oftedal OT and Allen ME: The feeding and nutrition of omnivores with emphasis on primates, in Kleiman DG, Allen ME, Thompson KV, Lumpkin S, and Harris H (eds): Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, 1996, pp 148–157.
- 11. Troyer K: Structure and function of the digestive tract of a herbivorous lizard, *Iguana iguana*. *Physiol. Zool.* 57:1–8, 1984.
- 12. Allen ME, Oftedal OT, and Werner DI: Management of the green iguana (*Iguana iguana*) in Central America. *Proc. Amer. Assoc. Zoo Vet.*, 1990, pp 19–22.
- van Marken Lichtenbelt WD: Optimal foraging of a herbivorous lizard, the green iguana. Oecologia (Berlin) 95:246–256, 1993.
- Werner DI: Research on management of an endangered species in Panama: the green iguana. Biol. Conserv. News. 21:1-12, 1984.
- Werner DI: Iguana management in Central America. Board on Science and Technology for International Development 6:4-6, 1985.
- 16. Allen ME, Oftedal OT, Baer DJ, and Werner D: Nutritional studies with the green iguana, in Meehan TP, Thompson SD, and Allen ME (eds): Proc. Eighth Dr. Scholl Conf. Nutrition of Captive Wild Animals. Lincoln Park Zoological Gardens, Chicago, 1991, pp 73–81.
- 17. Fitch HF, Henderson RW, and Hillis DM: Exploitation of iguanas in Central America. In Burghardt GM and Rand AS (eds): *Iguanas of the World: Their Behavior, Ecology, and Conservation*. Noyes Publications, Park Ridge, NJ, 1982, pp 397–417.
- Bernard JB, Oftedal OT, Barboza PS, Mathias CE, Allen ME, Citino SB, Ullrey DE, and Montali RJ: The response of vitamin-D deficient green iguanas (*Iguana* iguana) to artificial ultraviolet light. *Proc. Amer. Assoc.* Zoo Vet., 1991, pp 147–150.
- 19. Baer DJ: Effects of diet composition and ambient temperature on digestive function and bioenergetics of the green iguana (Iguana iguana), PhD thesis. Michigan State University, East Lansing, MI, 1992.
- Bernard JB: Spectral irradiance of fluorescent lamps and their efficacy for promoting vitamin D synthesis in herbivorous reptiles, PhD thesis. Michigan State University, East Lansing, MI, 1995.
- 21. Allen ME, Oftedal OT, and Horst RL: Remarkable differences in the response to dietary vitamin D among species of reptiles and primates: ls ultraviolet B light essential?, in Holick MF and Jung EG (eds): *Biologic Effects of Light 995*. Walter de Gruyter, New York, 1996, pp 13–38.
- 22. Oftedal OT and Allen ME: Nutrition as a major facet of reptile conservation. *Zoo Biol.* 15:491–497, 1996.
- 23. Baer DJ, Oftedal OT, Rumpler WV, and Ullrey DE: Dietary fiber influences nutrient utilization, growth and

- dry matter intake of green iguanas (*Iguana iguana*). J. Nutrit. 127:1501–1507, 1997.
- Donoghue S: Growth of juvenile green iguanas (*Iguana iguana*) fed four diets. *J. Nutrit.* 124:2626S–2629S, 1995.
- 25. Oftedal OT and Ullrey DE: Personal communication.
- 26. Nagy K: Nitrogen requirement and its relation to dietary water and potassium content in the lizard *Sauromalus* obesus. J. Comp. Physiol. 104:49–58, 1975.
- 27. Oftedal OT, Allen ME, Chung AL, Reed RC, and Ullrey DE: Nutrition, urates and desert survival: Potassium and the desert tortoise (*Gopherus agassizii*). Proc. Amer. Assoc. Zoo Vet. 1994:308–313.
- 28. Dantzler WH: Renal function (with special emphasis on nitrogen excretion), in Gans C and Dawson W (eds): Biology of the Reptilia: Physiology A. Vol. 5. Academic Press, London and New York, 1976, pp 447–503.
- Minnich JE: Excretion of urate salts by reptiles. Comp. Biochem. Physiol. [A] 41:535-549, 1972.
- Frye FL: Biomedical and Surgical Aspects of Captive Reptile Husbandry. Veterinary Medicine Publishing Co., Edwardsville, KS, 1981.
- 31. Ullrey DE, Allen ME, and Baer DJ: Formulated diets versus seed mixtures for psittacines. *J. Nutrit.* 121: S193-S205, 1991.
- 32. Amand WB: Avian clinical hematology and blood chemistry, in Fowler ME (ed): Zoo and Wild Animal Medicine. 2nd ed. WB Saunders Co., Philadelphia, 1986, pp
- Marks SK and Citino SB: Hematology and serum chemistry of the radiated tortoise (*Testudo radiata*). J. Zoo Wildl. Med. 21:342–344, 1990.
- 34. Berkow R and Fletcher AJ (eds): The Merck Manual of Diagnosis and Therapy. 16th ed. Merck Research Laboratories, Rahway, NJ, 1992.
- 35. Maixner JM, Ramsay EC, and Arp LH: Effects of feeding on serum uric acid in captive reptiles. *J. Zoo Anim. Med.* 18:62–65, 1987.
- Raphael BL, Calle PP, Stetter MS, Mangold B, and Cook RA: Normal variations in selected plasma biochemicals of reptiles. *Proc. Amer. Assoc. Zoo Vet.*, 1995, pp 233–235.
- 37. Hamdoun A and Frye FL: Observations on the growth of juvenile green iguanas *Iguana iguana* fed four commercial diets. *Vivarium* 7(2):50–53, 1995.
- 38. Guard CL: The reptilian digestive system: general characteristics, in Schmidt-Nielsen K, Bolis L, and Taylor CR (eds): Comparative Physiology: Primitive Mammals. Cambridge University Press, New York, 1980, pp 43–51.
- 39. McBee RH and McBee VH: The hindgut fermentation in the green iguana, *Iguana iguana*, in Burghardt GM and Rand AS (eds): *Iguanas of the World: Their Behavior, Ecology and Conservation*. Noyes Publication, Park Ridge, NJ, 1982, pp 77–83.
- 40. Van Soest PJ: Nutritional Ecology of the Ruminant. 2nd ed. Cornell University Press, Ithaca, NY, 1994.
- 41. Allen ME and Oftedal OT: Essential nutrients in mammalian diets, in Kleiman DG, Allen ME, Thompson

- KV, Lumpkin S, and Harris H (eds): Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, 1996, pp 117-128.
- 42. King G: Reptiles and Herbivory. Chapman & Hall, London, 1996.
- 43. Bjorndal KA, Bolten AB, and Moore JE: Digestive fermentation in herbivores: effect of food particle size. Physiol. Zool. 63:710-721, 1990.
- 44. Wallach JD and Hoessle C: Fibrous osteodystrophy in green iguanas. J. Amer. Vet. Med. Assoc. 153:863-865, 1968.
- 45. Wallach JD and Hoff GL: Metabolic and nutritional diseases of reptiles, in Hoff GL and Davis JW (eds): Noninfectious Diseases of Wildlife. Iowa State University Press, Ames, IA, 1982, pp 155-167.
- 46. Russo EA: Nutritional osteodystrophy in an iguana. Av. /Exot. Prac. 2 (No. 2):14-20, 1985.
- 47. Dacke CG: Calcium Regulation in Sub-Mammalian Vertebrates. Academic Press, London, 1979.
- 48. Guyton A: Textbook of Medical Physiology. 8th ed. WB Saunders Co., Philadelphia, 1991.
- 49. Allen ME: Nutritional aspects of insectivory, PhD thesis. Michigan State University, East Lansing, MI, 1989.
- 50. Anderson MP and Capen CC: Ultrastructural evaluation of parathyroid and ultimobranchial glands in iguanas with experimental nutritional osteodystrophy. Gen. Comp. Endocrin. 30:209-222, 1976.
- 51. Anderson MP and Capen CC: Fine structural changes of bone cells in experimental nutritional osteodystrophy of green iguanas. Virchows Arch. B Cell Path. 20:169-184, 1976.
- 52. Webb AR and Holick MF: The role of sunlight in the cutaneous production of vitamin D3, in Olson RE, Beutler E, and Broquist HP (eds): Annual Review of Nutrition. Annual Reviews, Palo Alto, CA, 1988, pp 375–399.
- 53. Richman L, Montali R, Allen M, and Oftedal O: Widespread metastatic soft tissue mineralization in vitamin D deficient green iguanas (Iguana iguana). Vet. Path. 32:560, 1995.
- 54. Richman LK, Montali RK, Allen ME, and Oftedal OT: Paradoxical pathologic changes in vitamin D deficient green iguanas (Iguana iguana). Proc. Amer. Assoc. Zoo Vet., 1995, pp 231–232.
- 55. Jackson OF and Cooper JE: Nutritional diseases, in Cooper JE and Jackson OF (eds): Diseases of the Reptilia. Vol. 2. Academic Press, London and New York, 1981, pp 409-428.
- 56. Collins ED and Norman AW: Vitamin D, in Machlin LJ (ed): Handbook of Vitamins. 2nd ed. Marcel Dekker, lnc., New York, 1991, pp 59-98.
- 57. Wiewandt TA: Evolution of nesting patterns in iguanine lizards, in Burghardt GM and Rand AS (eds): Iguanas of the World: Their Behavior, Ecology, and Conservation. Noves Publications, Park Ridge, NJ, 1982,
- 58. National Research Council: Vitamin Tolerance of Animals. National Academy of Sciences, Washington, DC,
- 59. Fraser DR: Vitamin D. Lancet 345:104-107, 1995.

- 60. Ullrey DE and Bernard JB: Vitamin D metabolism. sources, unique problems in zoo animals, meeting needs, in Fowler ME (ed): Zoo and Wild Animal Medicine. WB Saunders Co., Philadelphia, In Press.
- 61. Power ML, Oftedal OT, Savage A, Blumer S, Soto LH. and Holick MF: Assessing vitamin D status of Callitrichids: Baseline data from wild cotton top tamarins (Saguinus oedipus) in Columbia. Zoo Biol. 16:39-46,
- 62. Tian XQ, Chen TC, Allen M, and Holick MF: Photosynthesis of previtamin D₃ and its isomerization to vitamin D₃ in the savanna monitor lizard, in Norman AW, Bouillon R, and Thomasset M (eds): Vitamin D, a Pluripotent Steroid Hormone: Structural Studies, Molecular Endocrinology and Clinical Applications. Walter de Gruyter, Berlin, 1994, pp 893-894.
- 63. Holick MF, Tian XQ, and Allen M: Evolutionary importance for the membrane enhancement of the production of vitamin D₃ in the skin of poikilothermic animals. Proc. National Acad. Sci. 92:3124-3126, 1995.
- 64. Correll DL, Clark CO, Goldberg B, Goodrich VR, Haves DR, Klein WH, and Schecher WD: Spectral ultraviolet-B radiation fluxes at the earth's surface: Long-term variation at 39 N, 77 W. J. Geophys. Res. 97:7579-7591, 1992.
- 65. Gehrmann WH: Ultraviolet irradiances of various lamps used in animal husbandry. Zoo Biol. 6:117-127, 1987.
- 66. Laing CJ, Trube A, Shea GM, Fraser DR: The requirement for natural sunlight to prevent vitamin D deficiency in iguanian lizards. J. Zoo Wild. Med. 32(3):342-348, 2001.
- 67. Troyer K: Transfer of fermentative microbes between generations in a herbivorous lizard. Science 216:540-
- 68. National Research Council: Nutrient Requirements of Poultry. 9th ed. National Academy Press, Washington. DC, 1994.
- 69. Scott ML, Nesheim MC, and Young RJ: Nutrition of the Chieken. 3rd ed. ML Scott & Assoc., Ithaca, NY, 1982.
- 70. Gubler CJ: Thiamin, in Machlin LJ (ed): Handbook of Vitamins. 2nd ed. Marcel Dekker, Inc., New York, 1991, pp 233-281.
- 71. Chatterjee IB, Majumder AK, Nandi BK, and Subramanian N: Synthesis and some major functions of vitamin C in animals. Ann. New York Acad. Sci. 258:24-47, 1975.
- 72. Vosburgh KM, Brady PS, and Ullrey DE: Ascorbic acid requirements of garter snakes: Plains (Thamnophis radix) and eastern (T. sirtalis sirtalis). J. Zoo Anim. Med. 13:38-42, 1982.
- 73. Hanssen I, Grav HJ, Steen JB, and Lysnes H: Vitamin C deficiency in growing willow ptarmigan (Lagopus lagopus lagopus). J. Nutrit. 109:2260-2276, 1979.
- 74. Moser U and Bendich A: Vitamin C, in Machlin LJ (ed): Handbook of Vitamins. 2nd ed. Marcel Dekker, Inc., New York, 1991, pp 195-232.
- 75. Allen ME and Oftedal OT: The nutrition of carnivorous reptiles, in Murphy JB, Adler K, and Collins JT (eds): Captive Management and Conservation of Amphibians

- and Reptiles. Soc. Study Amphib. Reptil., Ithaca, NY, 1994, pp 71–82.
- 76. Larsen RE, Buergelt C, Cardeilhac PT, and Jacobson ER: Steatitis and fat necrosis in captive alligators. *J. Amer. Vet. Med. Assoc.* 183:1202–1204, 1983.
- 77. Farnsworth RJ, Brannian RE, Fletcher KC, and Klassen S: A vitamin E-selenium responsive condition in a green iguana. *J. Zoo Anim. Med.* 17:42–43, 1986.
- 78. Behrens WA and Medere R: Tissue discrimination between dietary RRR-alpha- and all rac-alpha-tocopherols in rats. *J. Nutrit.* 121:454–459, 1991.
- Craig AM, Blythe LL, Lassen ED, Rowe KE, Barrington R, and Slizeski M: Variations in serum vitamin E, cholesterol and total serum lipid concentrations in horses during a 72-hour period. Amer. J. Vet. Res. 50:1527– 1531, 1989.
- Ullrey DE and Allen ME: Principles of zoo mammal nutrition, in Fowler ME (ed): Zoo and Wild Animal Medicine.
 2nd ed. WB Saunders Co., Philadelphia, 1986, pp 515–532.
- 81. Pappas AM, Cambre RC, Citino SB, Baer DJ, and Wooden GR: Species differences in the utilization of various forms of vitamin E. *Proc. Amer. Assoc. Zoo Vet.*, 1990, pp 186–192.
- Mertz W (ed): Trace Elements in Human and Animal Nutrition. Vol. 1, 5th ed. Academic Press, Inc., New York, 1987.

- Mertz W (ed): Trace Elements in Human and Animal Nutrition. Vol. 2, 5th ed. Academic Press, Inc., New York, 1987.
- 84. National Research Council: *Mineral Tolerance of Domestic Animals*. National Academy of Sciences, Washington, DC, 1980.
- National Research Council: Nutrient Requirements of Sheep. 6th ed. National Academy Press, Washington, DC, 1985.
- Kingsbury JM: Poisonous Plants of the United States and Canada. Prentice-Hall, Englewoood Cliffs, NJ, 1964.
- 87. Hodgkinson A: Oxalic Acid in Biology and Medicine. Academic Press, London, 1977.
- 88. Barry TN and Blaney BJ: Secondary compounds of forages, in Hacker JB and Ternouth JH (eds): *The Nutrition of Herbivores*. Academic Press, Sydney, 1987, pp 91–119.
- Cheeke PR and Shull LR: Natural Toxicants in Feeds and Poisonous Plants. AVI Publishing Co., Westport, CT, 1985.
- 90. Norton TM, Jacobson ER, Caliguri R, and Kollias GV: Medical management of a Galapagos tortoise (*Geochelone elephantopus*) with hypothyroidism. *J. Zoo Wildl. Med.* 20:212–216, 1989.
- 91. Donoghue S and Langenberg J: Nutrition, in Mader DR (ed): *Reptile Medicine and Surgery*. WB Saunders Co., Philadelphia, 1996, pp 148-174.