

Review Article

Nutrition of Birds in the Order Psittaciformes: A Review

Elizabeth A. Koutsos, MS, Kevin D. Matson, MS, and Kirk C. Klasing, MS, PhD

Abstract: Over 350 species of birds make up the order Psittaciformes; many of these are maintained in captive environments. Malnutrition is commonly diagnosed in captive psittacine birds; therefore, providing nutritionally adequate diets must be a primary concern. This review integrates quantitative information on the dietary habits and nutritional requirements of psittacine birds to facilitate the formulation and evaluation of diets for birds in captivity. Initially, characterization of the diet and feeding strategy of a particular species in the wild can provide insight into appropriate diet choices in captivity. Knowledge of the gastrointestinal anatomy and physiology can be used to elucidate the capacity of that species to utilize various feedstuffs. For example, the presence of a highly muscularized gizzard may allow a bird to utilize a seed-based diet, whereas a species possessing a small gizzard may be unable to process such a diet. Finally, nutrient requirements determined in a particular species or a related species (eg, similar digestive physiology and feeding strategy) may be applied to create a nutritionally adequate diet. Understanding the factors involved in selecting appropriate diets enables aviculturists, veterinarians, and nutritionists to maintain and propagate these birds with increased success.

Key words: nutrition, requirements, diets, avian, psittacine, Psittaciformes

Introduction

The order Psittaciformes has 2 families, the Cateulidae with 21 species (including cockatoos, cockatiels, and corellas) and the Psittacidae with 331 species (including lorries, lorikeets, parrots, macaws, parakeets, parrots, rosellas, and lovebirds).¹ These species are found primarily in many tropical and subtropical environments around the world, as well as in temperate climates in New Zealand and southern Australia. Many of these species are kept in captivity as companions and display specimens and for conservation purposes. Proper nutrition of psittacine birds is essential, and malnutrition is one of the most clinically relevant health issues.^{2,3} In fact, many commonly fed captive diets are deficient in 1 or more essential nutrients.^{4,5}

The evolution of nutrition for psittacine birds has followed 3 stages. Early diets were based upon food habits of wild birds. Next, nutrient require-

ments that were scientifically determined for poultry were adopted, at least in part, as standards for diets of captive psittacine birds. We are now in a third phase in which research populations of easily propagated species, such as budgerigars (*Melopsittacus undulatus*) and cockatiels (*Nymphicus hollandicus*), are being used to investigate dietary preferences, nutrient requirements, and metabolic capabilities.

The goal of this review is to integrate known quantitative information on the dietary needs of psittacine birds so the diets of captive birds can be formulated and evaluated. Because the requirements for only a few of the more than 40 required nutrients have been determined in psittacine birds, we will likely be dependent upon the known requirements of poultry⁶ for many years to come. Extrapolations of requirements developed in 1 avian species to other species should be based on the gastrointestinal morphology of the target species, the diet specializations of free-living members of that species, and experience gained by aviculturists and veterinarians. These latter 2 areas have been summarized in several excellent reviews.^{7–14}

From the Department of Animal Science, University of California, Davis, CA 95616, USA (Koutsos, Klasing); and the Department of Biology, University of Missouri, Saint Louis, MO 63121-4499, USA (Matson).

Nutritional Ecology and Diets of Wild Psittacine Birds

The dietary feeding strategy of an animal (ie, the type of food consumed in the wild) is a valuable nutritional tool used to classify groups of animals. In general, most birds in the order Psittaciformes consume plant-based diets, and they are classified as florivores. Within this general category, further subclassifications can be made on the basis of the primary types of parts of plants consumed. Common psittacine subclassifications include granivory (grain or seed-based diet, including budgerigars and cockatiels), frugivory (fruit-based diet, including many macaws), and nectarivory (nectar-based diet, including lorikeets and lories).¹⁵ Within the category of granivorous birds, smaller birds tend to select grass seeds and larger birds tend to select increased proportions of seeds from shrubs, which contain higher levels of protein.^{16,17}

In contrast to birds that specialize on 1 specific feed type, many psittacine birds consume more diverse diets, including foodstuffs from 2 or more categories. Frugivorous-granivorous psittacine birds are commonly described and include the red-fronted macaw (*Ara rubrogenys*), regent's parrot (*Polytelis anthopeplus*), and scarlet macaw (*Ara macao*).^{18–20} Species commonly considered nectarivores, such as the rainbow lorikeet (*Trichoglossus haematodus*) and Stephen's lory (*Vini stepheni*), often feed on other dietary items, including fruits, seeds, and insects.^{21,22} Finally, many psittacine birds eat a large variety of ingredients that include animal matter and are best categorized as omnivorous (including many cockatoos and parakeet species). Psittaciformes classifications by feeding strategy and common diet ingredients are listed in Table 1.

Whereas dietary classifications can be made from observations of feeding behavior in the wild, diet ingredients selected by psittacine birds have been shown to vary over time depending on nutrient availability^{23,24} and sex of the bird²³ and between age classes.²⁵ Another important distinction in selection of foodstuffs by these birds is their ability to adapt to and exploit introduced, nonnative, or domesticated sources of food. The budgerigar, cockatiel, rose-ringed parakeet (*Psittacula krameri*), red-fronted macaw, regent's parrot, golden parakeet (*Aratinga guarouba*), kakapo (*Strigops habroptilus*), and hooded parrot (*Psephotus dissimilis*)^{19,20,26–31} have been reported to eat nonnative plant matter, most commonly from grain crops and introduced ornamentals and fruit trees. In contrast, some psittacine birds are very specific about the foods they consume in the wild. On the basis of field obser-

vations and gastrointestinal tract contents, the glossy black-cockatoo (*Calyptorhynchus lathami halmaturinus*) feeds almost entirely on seeds of a single species of native tree (*Allocasuarina verticillata*), the forest red-tailed black cockatoo (*Calyptorhynchus banksii naso*) eats the seeds of only 2 native trees (*Corymbia calophylla* and *Eucalyptus marginata*),^{27,32} and the vulturine parrot (*Psittarchas fulgidus*) is a specialized frugivore that consumes the fruit of only 1 or 2 of the 38 extant species of figs (*Ficus* species) in its native New Guinea.³³ Finally, the amount of time spent foraging and/or feeding per day varies depending on the species being considered. In general, parrots actively feed in 2 sessions—1 in the morning and 1 in the evening.^{20,27,30} One species, the forest red-tailed black cockatoo, was reported to eat not in 2 distinct bouts but in 1 long daily feeding period.³⁴ In many species, including the kaka (*Nestor meridionalis septentrionalis*), pacific parakeet (*Aratinga strenua*), and ground parrot (*Pezoporus wallicus*), foraging and feeding represent the majority (> 50%) of daily activities.^{23,25,35}

Functional Digestive Anatomy

The digestive anatomy of an animal generally reflects the type of diet it consumes, and the feeding strategies of psittacine species (granivory, frugivory, nectarivory, and omnivory) are reflected in these birds' gastrointestinal morphology.

Psittacine digestive tracts (GI tract), like those of other avian species, begin at the beak, followed by a toothless mouth, tongue, pharynx, esophagus, crop, proventriculus, gizzard, intestine, rectum, cloaca, and vent.^{15,36–38} Accessory organs include the biliary and salivary systems, pancreas, intestinal lymphoreticular tissue, and bursa. Each portion of the digestive tract provides function for acquiring, digesting, and absorbing nutrients or for immunocompetence.¹⁵

Acquisition of food is enabled by the beak, tongue, and oral cavity. In addition, the psittacine beak is used for preening feathers, climbing, courtship, parental behavior, and defense.³⁶ Beak shape and size are often adapted to accommodate preferred foods, allowing for more efficient use of the beak. For example, granivorous birds often have defined ridges on the edges of their beaks that are used for seed cracking,³⁹ and an articulation of the maxillary beak to the skull permits increased gape diameter and absorption of the shock from cracking the hull of seeds.

The tongues of psittacine birds contain a medial groove from the glottis to the tip⁴⁰ and have a well-

Table 1. Feeding strategies and common diet ingredients of wild birds in the order Psittaciformes.

Species name	Feeding strategy	Common diet ingredients ^a	Time spent feeding ^b	Reference
Blue and gold macaw (<i>Ara ararauna</i>)	florivore	seeds, fruits, nuts	NR	18
Kaka (<i>Nestor meridionalis septentrionalis</i>)	florivore	1° insects, seeds, nectar/pollen, fruit, sap	>50% of day foraging	23
Kakapo (<i>Strigops habroptilus</i>)	florivore	1° leaves, also mosses, rhizomes, roots, bark, fruit	NR	31
Military macaw (<i>Ara militaris</i>)	florivore	seeds, nuts, berries, fruits	NR	18
Pacific parakeet (<i>Aratinga strenua</i>)	florivore	fruits, seeds, flowers (dry season); grains, fruits (wet)	6–18 h/d	35
Red-faced parrot (<i>Hapalopsittaca pyrrhops</i>)	florivore	flowers, berries, shoots, seeds, seed pods	NR	115
Scaly-headed parrot (<i>Pionus maximiliani</i>)	florivore	seeds (70%), flowers (20%), grain (8%), fruit pulp (2%)	NR	116
Blue-throated macaw (<i>Ara glaucogularis</i>)	frugivore	palm fruit, nuts, milk	NR	18
Buffon's macaw (<i>Ara ambigua</i>)	frugivore	fruits, flowers	NR	18
Golden parakeet (<i>Aratinga guarouba</i>)	frugivore	fruits, buds, flowers	NR	29
Green-winged macaw (<i>Ara chloroptera</i>)	frugivore	fruits (Hymenaea), palm nuts, seeds	NR	18
Orange-winged amazon (<i>Amazona amazonica</i>)	frugivore	fruit (85% from palm fruit)	NR	117
Red-bellied macaw (<i>Ara manilata</i>)	frugivore	fruit (96% from palm fruit, flowers, seed pods)	NR	117
Vulturine parrot (<i>Psittichas fulgidus</i>)	frugivore	1 or 2 of the 38 extant species of figs (<i>Ficus</i> species)	NR	33
Red-fronted macaw (<i>Ara rubrogenys</i>)	frugivore-granivore	fruits, seeds	1–4 h/d	20
Regent's parrot (<i>Polytelis anthopeplus</i>)	frugivore-granivore	fruit, seeds	NR	19
Scarlet macaw (<i>Ara macao</i>)	frugivore-granivore	fruits, nuts, bark, leaves, shoots	NR	18
Baudin's cockatoo (<i>Cacatua baudinii</i>)	granivore	seeds—1° from nuts of marri (<i>C calophylla</i>)	NR	118
Budgerigar (<i>Melopsittacus undulatus</i>)	granivore	seeds	NR	26
Carnaby's cockatoo (<i>Calyptorhynchus funereus latirostris</i>)	granivore	seeds (especially from cones and nuts of Proteaceae)	NR	118
Cockatiel (<i>Nymphicus hollandicus</i>)	granivore	seeds (prefers soft, young over mature, hard seeds)	3 h/d	27
Forest red-tailed cockatoo (<i>Calyptorhynchus banksii naso</i>)	granivore	seeds of two native trees (<i>C calophylla</i> and <i>E marginata</i>)	10–12 h/d	34
Glossy black cockatoo (<i>Calyptorhynchus lathami halmaturinus</i>)	granivore	seeds of a single native tree (<i>A verticillata</i>)	6.4–11 h/d	32, 119
Ground parrot (<i>Pezoporus wallicus</i>)	granivore	seeds, some insect larvae	most of the day	25
Hyacinth macaw (<i>Anodorhynchus hyacinthinus</i>)	granivore	palm nuts (50% lipid content)	NR	18
Lear's macaw (<i>Anodorhynchus leari</i>)	granivore	1° palm nuts, fruit	NR	18

Table 1. Continued.

Species name	Feeding strategy	Common diet ingredients ^a	Time spent feeding ^b	Reference
Pale-headed rosella (<i>Playcerus adscitus</i>)	granivore	seeds (3–73%), animal matter (0–26%) (varies with season)	NR	120
Red-fronted macaw (<i>Ara rubrogenys</i>)	granivore	nuts, seeds, fruit	NR	18
Red-tailed black cockatoo (<i>Calyptorhynchus magnificus samueli</i>)	granivore	seeds	NR	18
Rose-ringed parakeet (<i>Psittacula krameri</i>)	granivore	seeds	NR	28, 121
Spix's macaw (<i>Cyanopsitta spixii</i>)	granivore	palm nuts	NR	18
Palm cockatoo (<i>Probosciger terrimus</i>)	granivore- frugivore	seeds, fruit, seeds from fruits eaten by cassowaries	NR	122
Rainbow lorikeet (<i>Trichoglossus haematodus</i>)	nectarivore	1° nectar, pollen, fruits, seeds	NR	22
Stephen's lory (<i>Vini stepheni</i>)	nectarivore	nectar, pollen, fruit, insects (1° lepidopteran larvae)	NR	21
Corella (<i>Cacatua pastinator</i>)	omnivore	1° grains and seeds (up to 80%), some insect larvae	NR	123, 124
Eastern rosella (<i>Platycercus eximius</i>)	omnivore	seeds (3–73%, animal matter (0–50%) (varies with season)	NR	125
Hooded parrot (<i>Psephotus dissimilis</i>)	omnivore	1° seeds (1° sesame), flowers, invertebrates	NR	30
Major Mitchell cockatoo (<i>Cacatua leadbeateri</i>)	omnivore	larvae, fruits, seeds	NR	118
Black cockatoo (<i>Calyptorhynchus</i> species)	omnivore	1° seeds, fruits, flowers, insects/larvae, pine cones	NR	119
Red-crowned parakeet (<i>Cyanoramphus novaezelandiae</i>)	omnivore	1° flowers, seeds, also fruit, vegetation, invertebrates	NR	24
Red-tailed amazon (<i>Amazon brasiliensis</i>)	omnivore	seed, fruits, flowers, leaves, nectar, insects	NR	126
Sulphur-crested cockatoo (<i>Cacatua galerita</i>)	omnivore	seeds (1° sunflower), grubs, rhizomes	NR	118
Yellow-crowned parakeet (<i>Cyanoramphus auriceps auriceps</i>)	omnivore	1° invertebrates, also plant matter	NR	24, 127

^a 1° = primary.

^b NR indicates not reported; h/d = hours/day.

developed lingual nail, consisting of a stiff cuticle covering of the ventral and lateral surfaces of the tongue.^{39,41} Furthermore, these birds have specialized muscles associated with the lingual nail and apex of the tongue that allow for enhanced flexibility and food manipulation, complementing the functions of the hyoid apparatus used by most other birds for tongue mobility.^{39,42} Slight differences in tongue anatomy may be found between psittacine species. For example, species in the subfamily *Loriinae* (lorikeets) consume pollen and nectar from flowers and have tongues that are longer and narrower than those of granivorous and frugivorous parrots.⁴³

The flexibility and muscularity of the tongue permit its use by psittacine birds to aid in drinking.

Four general drinking methods have been described⁴²: *Cacatuidae* (cockatoos), scoop water with the lower bill and flush it back with the tongue; *Loriinae*, lap water with the brush-tipped tongue; *Psittacinae*, ladle water with the tip of the tongue, which is then pressed into the palate to move the water back; *Psittichadinae* and *Loriculinae*, keep the tongue pressed against the palate and drink with a suction-pump action.

Touch receptors, which confer strong tactile sense, are found in rich supply on the tongue, oral cavity, and beak. In contrast, avian taste buds, found in the oral cavity on the floor of the pharynx and the base of the tongue,⁴⁴ are found in much lower numbers than those in mammals. Parrots have been reported to have 350 taste receptors, compared with

9000 in humans.⁴⁵ These data suggest that birds generally have poorer taste acuity than mammals. Despite the paucity of taste buds, taste has been demonstrated to be an important factor in determining food acceptance and avoidance for birds. Nectarivores differentiate between sugar solutions based on composition^{46,47} and concentration.⁴⁸ Secondary plant compounds such as tannins prevent some florivorous species from eating certain plant food-stuffs,⁴⁹ and common defense secretions of insects are effective in repelling birds at very low concentrations (1:4000).⁵⁰

Recent studies on cockatiels suggest that their gustatory abilities are quite variable and depend on the compound being tested.^{51,52} For instance, these birds are particularly insensitive to 3 common sugars (sucrose, fructose, glucose), with thresholds ranging from 0.16 to 0.40 mol/L, but particularly sensitive to representative plant secondary compounds (quinine, gramine, and tannins), with thresholds ranging from 0.0001 to 0.01 mol/L (K. D. M., unpublished data, February 2001). Cockatiels, and other birds, typically reject salts around the point of osmolarity.^{51–54} Put in context, the ability of cockatiels to taste quinine nears the threshold of humans, whereas the same birds are much less sensitive than humans to fructose. These data concerning avian gustatory abilities suggest that cockatiels are more sensitive to those “ecologically relevant” compounds (ie, toxic secondary compounds in the case of a granivore, sugars for nectarivores, etc) and less sensitive to those compounds that are unlikely to be encountered. These studies also suggest that some species may have keener abilities of nutrient detection, whereas others have sharper toxin avoidance capacities. Recent research indicates that the transduction pathways of some taste receptors are plastic and adaptable rather than passive as once thought. This plasticity may endow these receptor cells with the ability to regulate taste responses in relation to nutritional status.⁵⁵

Once food leaves the oral cavity, it enters the esophagus, which is expandable to allow large food items to be swallowed. The esophagus widens into the crop, which consists of a thick, cornified epithelium that protects the bird from damage resulting from swallowing whole foods. This region allows for softening of food to enable more efficient digestion of feedstuffs, as well as regurgitation of softened food to chicks. Crop capacity has been shown to change seasonally; the crop of the purple-crowned lorikeet (*Glossopsitta porphyrocephala*) holds almost half of the contents of the entire GI tract when nectar is highly available, although crop volume decreases to less than half this size during

periods when nectar is unavailable and pollen is the primary food source.⁴⁰

The proventriculus and gizzard of psittacine birds are variable in their functional anatomy. The proventriculus contains gastric glands that produce HCl and pepsin, which begin to break down and emulsify foods. In budgerigars, the gastric glands are coiled and branched tubular complexes served by a single duct each.⁵⁶ The gizzard of granivorous species is large and muscular, with a thick interior keratin lining; nectarivorous species tend to have a smaller, less developed gizzard.⁴³ Digestion of pollen is not thought to require crushing by the gizzard,⁵⁷ and consequently quick passage through this organ probably does not reduce digestibility. In nectarivores, access in and out of the proventriculus and gizzard lies in the same medial plane as the entrance to the duodenum. This arrangement facilitates quick processing of highly digestible nectar but presumably diminishes the capacity to digest seeds and hard-bodied insects.

Once food particles are broken down and partially emulsified, the digesta moves into the small intestine. The primary functions of the small intestine are enzymatic digestion and nutrient absorption.³⁶ Pancreatic enzymes hydrolyze most starches, proteins, and nucleic acids in foods, but the proportion of enzymes released during a meal varies with species.⁵⁸ The presence of lactase has not been demonstrated, rendering lactose-containing foods indigestible. Nutrient absorption occurs across the intestinal villi into the enterocytes. By enhancing surface area, the villi facilitate nutrient absorption in this region. Some frugivorous species and nectarivorous species have exceptionally long (7 μm) intestinal microvilli,³⁸ which presumably aids in absorption of the free sugars found in their food. Villi extend into the rectum and coprodeum of budgerigars but not many other species.⁵⁶

The ceca of birds in the order Psittaciformes are absent or vestigial,⁵⁹ resulting in little or no hindgut fermentation of poorly digestible carbohydrates. Therefore, the small intestine terminates at the rectum, which empties into the cloaca. The cloaca serves as a storage site for urine and feces. In many avian species, retrograde movement of urine from the cloaca to the rectum allows for resorption of protein, salts, and water; this phenomenon likely occurs in psittacine birds as well.

The average length of time that food is retained in the GI tract (mean retention time) depends upon food characteristics, feeding strategy, digestive anatomy, and body size. In general, larger birds have longer GI tracts and retention times. The rate of passage of digesta in psittacine birds has not been

well studied. However, across avian nectarivores, typical mean retention time is approximately 30–50 minutes (but it is 80 minutes in rainbow lorikeets),⁶⁰ whereas in granivores retention times are approximately 40–100 minutes, and in frugivores retention times are approximately 15–60 minutes.^{15,61} The mean retention time is typically an order of magnitude shorter than the time required for complete evacuation of the GI tract. Complete evacuation of a single meal from the crop of a budgerigar takes 11.75 hours, whereas complete evacuation of the entire tract takes 26 hours.⁶²

Nutrient Requirements

Water

Often forgotten, but easily the most critical nutrient for most species, water is essential for maintenance of cellular homeostasis, epithelial integrity, food digestion, waste excretion, hygiene, and numerous metabolic reactions. The exact quantity required each day is dependent upon body size, diet, and environmental temperature. In general, birds conserve water very effectively because feathers minimize evaporative losses and excretory losses are low because of the effectiveness of the renal–cloacal complex. In budgerigars at thermoneutral temperatures, about 35% of daily water loss occurs via excretion and 65% via evaporation.⁶³ Very small granivorous birds can survive without any drinking water because they produce sufficient water metabolically through oxidation of carbohydrate and fats to replace water losses. The budgerigar (27 g) and Bourke's parrot (*Neophema bourkii*; 39 g) can live without drinking water at cool temperatures (10–20°C)⁶⁴ but require drinking water at higher temperatures. Larger species require a water source at all environmental temperatures. MacMillen and Baudinette⁶⁴ determined the water requirement of adult parrots (ranging from 48 to 295 g) to be approximately 2.4% of body weight.

As environmental temperatures rise, water requirements increase. Physiologically, this change in requirements is due to increased water evaporation from the skin and the lungs as the bird cools itself by panting. For example, monk parakeets (*Myiopsitta monachus*) housed at 45°C have 12 times the rate of evaporative water loss compared with birds housed at 30°C.⁶⁵ Though some evaporative water loss is replaced by metabolic water, most must come from drinking water, and the amount of drinking water consumed would be expected to increase by a factor of about 10-fold in very hot weather.

When water is freely available, most birds drink considerably more water than the minimum

amounts described above. For example, budgerigars, which have no requirement for drinking water, choose to consume an average of 4 ml water/day.⁶⁶ There is also considerable individual variation in water consumption, and polydipsia can be psychogenic.⁶⁷ In our colony at University of California, Davis, cockatiels (93 g), which require approximately 2.5 ml water/d actually consumed an average of 13.6 ml/d.⁶⁸ Variation in water intake between birds was very high (4.5–31.5 ml/d, coefficient of variation = 51%), although individual birds tended to consume similar amounts of water each day (average coefficient of variation for each bird = 18.6%). Similarly, high variability has also been described in lovebirds and cockatoos.⁶⁹ Birds consuming fresh fruits and vegetables, which are often in excess of 85% water, would be expected to consume much lower than expected levels of drinking water. Clearly this huge variation in water intake makes medication or nutrient supplementation via the drinking water ill advised unless accurate information on the consumption of individual birds is known.

Energy

The maintenance energy requirement is the amount of dietary metabolizable energy (ME) needed to support basal metabolism, as expressed by basal metabolic rate (BMR), plus additional energy to fuel activity and thermoregulation. Growing birds also need energy to support the accretion of new tissues, reproducing birds need additional energy for accretion of gametes, and molting birds need energy to support feather growth.¹⁵ Obviously, the total energy requirements vary depending upon the environment, stage of life cycle, and genetics of the individual. Knowledge of energy requirements is very important because they are the primary factor that determines the amount of diet that should be fed or will be voluntarily consumed.¹⁵

A large number of studies have examined the BMR of psittacine birds. McNab and Salisbury⁷⁰ analyzed available data and concluded that the BMR of psittacine birds is dependent upon the thermal climate of the species' origin but is unrelated to food habits or water availability. Species originating from tropical climates have BMRs similar to those of other nonpasserines (BMR [kcal/d] = 73.6 × body weight [kg]^{0.73}; [kJ/d] = 308 × body weight [kg]^{0.73}). Species originating from temperate climates of New Zealand and Australia have a BMR that is 21% higher than tropical species.

Though research has provided us with accurate estimates of the BMR of Psittaciformes species,

birds expend this level of energy only when sleeping. Even the act of alertly perching increases energy expenditure by about twofold in budgerigars.⁷¹ Other activities like preening, eating, or shuffling locomotion increase energy expenditure by about 2.3-fold over BMR. Flight of budgerigars is especially expensive and requires 11 to 20 times more energy per minute than BMR.⁷² Buttemer et al⁷¹ closely observed budgerigars kept in large outdoor aviaries (12 × 6 × 4 m). These birds were more active in the wintertime than the summertime, but they still spent 94% of their time perching. The remainder of their activity was associated with preening (35 minutes/day), eating (34 minutes), shuffling around (10 minutes), and flying (5 minutes). In addition to energy required to support activity, thermoregulation requires significant amounts of energetic input, primarily at low ambient temperature. In the winter (average temperature of 5.9°C), daily energy requirements were 21% higher (24.1 kcal/d; [101 kJ/d] or 3.07 times BMR) compared with the summer (20.0 kcal/d [83.8 kJ/d] or 2.77 times BMR), when the temperature averaged 20.7°C.⁷¹ The thermoneutral zone of winter-adapted budgerigars ranged from 22 to 35°C, and summer-adapted birds began to expend additional energy for thermoregulation when the temperature went below 28°C. Finally, the energy requirements of free-living birds are typically greater than those of captive birds because of their extra costs for foraging for food, thermoregulation, and defenses. Williams et al⁷³ measured the daily energy expenditure of free-living Port Lincoln parrots (*Barnardius zonarius*) and galahs (*Cacatua roseicapilla*) when nesting and found that their daily ME requirements were 3.0 and 3.23 times BMR, respectively.

The energy requirements for chick growth will be based upon the fractional growth rate of that species. Birds in the order Psittaciformes are among the slowest growing of altricial species¹⁰ and also develop endothermy at an earlier age.⁷⁴ Thus, their energy requirements are likely to be more similar to precocial species than to highly altricial species, which grow faster and thermoregulate later. Kamphues and Wolf⁷⁵ measured the rate of protein and lipid gain in growing budgerigars (177 mg/d and 160 mg/d, respectively) and lovebirds (153 mg/d and 153 mg/d, respectively). Correcting these rates for the cost of deposition (10.8 kcal/g or 52 kJ/g) gives the additional energy needed for growth at 3.6 kcal/g (17.5 kJ/g) for budgerigars and 3.8 kcal/g (15.9 kJ/g) for lovebirds. Earle and Clarke⁶⁶ reported that the peak energy provisioned to budgerigar chicks was maximal about a week before fledging at 6.7 kcal/chick/day (28 kJ/chick/day).

Table 2. Estimation of metabolizable energy requirements for adult birds in the order Psittaciformes from body weight (BW).

Housing conditions ^a	Energy requirements	
	(kcal/d)	(kJ/d)
Indoor cage	154.6*BW ^{0.73}	647*BW ^{0.73}
Indoor aviary	176.6*BW ^{0.73}	739*BW ^{0.73}
Outdoor aviary, summer	203.9*BW ^{0.73}	853*BW ^{0.73}
Outdoor aviary, winter	226.1*BW ^{0.73}	946*BW ^{0.73}
Free living	229.2*BW ^{0.73}	959*BW ^{0.73}

^a Assumptions: birds housed in cages indoors are in thermoneutral zone and fly only minimally; birds in aviaries have the opportunity for short flights. Equations were derived from published estimates of basal metabolic rate (reference 128) and activity cost (references 71, 73) per kg BW.

Accurate daily energy requirements for captive psittacine birds are available only for budgerigars, which presents a problem for nutritionists concerned with other species. However, there is often a good correlation between daily energy expenditures and BMR.^{76,77} Relatively accurate and representative information on the BMR of Psittaciformes species can be used as a basis to calculate daily energy requirements. With this empirical approach, the BMR can be calculated for any species of interest on the basis of its body weight and the appropriate multiplication factor (Table 2).

The amount of food required to fulfill the energy requirement is dependent upon the density of metabolizable energy in that food and its digestibility. There appears to be a divergence in the digestive capacity of birds in the order Psittaciformes depending upon their dietary specialization. Granivorous and omnivorous species are comparatively efficient at obtaining energy from foods, whereas nectarivorous species are relatively inefficient (Table 3).

When provided ad libitum access to food, birds generally eat an amount that satisfies their daily energy expenditure. For example, red lorries (*Eos bornea*) are able to adjust their intake of nectars that contain variable energy densities so that their daily energy intake is constant.⁷⁸ Thus, when provided diets with lower than normal energy density (eg, high-fiber foods), animals increase the grams consumed each day, and, conversely, when presented a diet with high energy density (eg, high-fat foods), they decrease intake. However, the regulation of food intake is not always perfect, and obesity can result when diets with high energy densities are fed. For budgerigars, a diet containing 13 megajoules (MJ) of metabolizable energy (ME)/kg results in maintenance of body weight, but diets of 14 MJ/kg or

Table 3. Digestibility of diets by adult birds in the order Psittaciformes.

Species	Diet	Dry matter GE ^b (GE/g)	ME ^b (ME/g)	Assimilation efficiency (%)	Reference
Kaka	sunflower seeds, small amount of apple ^a	6.9 kcal/g (28.8 kJ/g)	5.4 kcal/g (22.7 kJ/g)	78.9	129
Kaka	insect larvae	8.1 kcal/g (33.9 kJ/g)	7.3 kcal/g (30.6 kJ/g)	91.16	129
Rainbow lorikeet	bread, honey, dried milk ^a	4.4 kcal/g (18.3 kJ/g)	3.9 kcal/g (16.3 kJ/g)	88.9	120
Budgerigar	corn, soybean meal ^a	4.2 kcal/g (17.5 kJ/g)	3.3 kcal/g (14.0 kJ/g)	80.0	83
Budgerigar	white millet	4.0 kcal/g (16.7 kJ/g)	3.7 kcal/g (15.6 kJ/g)	93.4	66
Budgerigar	red millet	3.7 kcal/g (15.5 kJ/g)	3.4 kcal/g (14.2 kJ/g)	92.0	66
Budgerigar	canary seed	3.3 kcal/g (14.0 kJ/g)	2.9 kcal/g (12.3 kJ/g)	88.2	66

^a Dietary proportions of each feedstuff not provided.

^b GE indicates gross energy; ME, metabolizable energy.

above resulted in obesity.⁷⁹ Ad libitum intake rates reported in the literature are summarized in Table 4.

Protein and amino acids

In general, avian species are unable to synthesize the "essential" amino acids arginine, isoleucine, leucine, lysine, methionine, phenylalanine, valine, tryptophan, and threonine. Glycine, histidine, and proline are often considered essential on the basis of research in chickens that demonstrated that rates of synthesis of these amino acids cannot meet metabolic demands.⁸⁰ As demonstrated in chickens, a requirement for glycine has been observed for the budgerigar,⁸¹ suggesting that psittacine birds are unable to synthesize enough glycine to meet metabolic demands. Furthermore, an essential level of protein must be included in the diet to meet nitrogen requirements of the animal. The quantitative requirement for amino acids is dependent upon the physiological state of the bird, being lowest in adults at maintenance and highest in hatchlings and females laying large clutches of eggs (Table 5). In the wild, some psittacine birds time their breeding to the seasonal availability of higher protein foods,⁸² indicating that amino acid nutrition is a major determinant of reproductive output. In captivity, cockatiels increased egg lay after protein content of the diet increased (E. A. K., unpublished data, February 2001).

For an adult bird in a nonbreeding, nonmolting maintenance state, amino acid and protein requirements are related to the rate of obligatory losses.¹⁵ Several experiments have been conducted to deter-

mine the amino acid requirements of small granivorous psittacine birds at maintenance. In budgerigars, 6.8% crude protein (0.33% sulfur amino acids, 0.15% lysine, 14.4 MJ ME/kg) maintained body weight,⁷⁹ but whether or not skeletal muscle mass was maintained is unclear. Underwood et al⁸³ found that a corn-based diet containing 12% protein (14.0 MJ ME/kg), but supplemented with lysine (0.29% methionine + cysteine, 0.63% lysine), was adequate to maintain weight and body composition of adult budgerigars. However, a seed-based diet with 12.8% protein that was low in lysine resulted in increased body fat. Because this seed-based diet was also clearly deficient in calcium and several trace nutrients, whether the problems with obesity were due to low amino acid levels or to other problems with a seed-based diet is not clear. In a trial with adult male cockatiels, 11% protein (soybean-based diet) supplemented with methionine (0.51% methionine + cysteine, 0.77% lysine) was adequate for maintenance of body weight and prevention of obesity.⁶⁸ These experiments indicate that the protein requirement for cockatiels and budgerigars is probably 11% or less if a high-quality protein source is used or if plant protein is supplemented with the first limiting amino acid (the amino acid found in the lowest proportion compared with dietary requirements). When seed protein sources are used, without supplementation, a higher level of protein would be required. Across granivorous avian species, the protein requirement (expressed as percentage of the diet) increases with increased body size¹⁵; therefore, higher levels of protein may be required by macaws and other larger psittacine birds. Preliminary exper-

Table 4. Reported food intake of captive adult birds in the order Psittaciformes.

Species	Environment	Diet (ME) ^a	Intake ^b (% BW/d)	Refer- ence
Budgerigar (<i>Melopsitticus undulatus</i>)	colony cages	corn/soy meal (3.3 kcal/g, 140 MJ/kg)	25%	83
Budgerigar	colony cages	millet, canary grass, oat groats	26%	83
Budgerigar	temperature-controlled room	Japanese millet	19.6%	62
Budgerigar	small cage	millet (2.9 kcal/g, 12.13 MJ/ kg)	14%	130
Rainbow lorikeet (<i>Trichoglossus haematodus</i>)	metabolism cage	sucrose/dextrin/egg white (4.0 kcal/g, 16.73 MJ/kg)	8.4%	86
Rainbow lorikeet	small cage	bread, honey, dried milk (4.4 kcal/g, 18.3 MJ/kg)	10.4%	120
African grey parrot (<i>Psittacus erithacus</i>)	small enclosure	extruded granules ^c (2.7 kcal/ g, 11.5 MJ/kg)	9.8%	112
Amazon parrots (<i>Amazon</i> species)	small enclosure	extruded granules ^c (2.7 kcal/g, 11.5 MJ/g)	6.2%	112
Lesser crested cockatoo (<i>Cacatua sulfurea sulfurea</i>)	small enclosure	extruded granules ^c (2.7 kcal/g, 11.5 MJ/g)	9.1%	112
Blue and gold macaw (<i>Ara ararauna</i>)	small enclosure	extruded granules ^c (2.7 kcal/g, 11.5 MJ/kg)	7.8%	112

^a Metabolizable energy (ME) content is based on values for chickens except when ME content of mixed seeds diets cannot be estimated because the proportion of seed consumption was not reported.

^b Dry matter intake, excluding hulls; BW indicates body weight.

^c Commercially available extruded granules, unknown composition.

iments with African gray parrots (*Psittacus erithacus*) suggest a requirement of between 10 and 15% protein to maintain plasma protein levels.⁸⁴

Obligatory nitrogen losses from the gastrointestinal tract are relatively low in nectarivorous (red

lories, *Eos bornea*) and frugivorous (Pesquet's parrots, *Psittichas fulgidus*) species compared with granivorous budgerigars,^{62,85} indicating that their protein requirement should also be lower. Frankel and Avram⁸⁶ examined dietary protein dynamics in

Table 5. Levels of protein and amino acid shown to be adequate for birds in the order Psittaciformes at a given physiological state.

Species	Physiological state	Protein source (ME level) ^a	Protein level	Reference
Budgerigar	maintenance	purified amino acids (3.4 kcal/g, 14.4 MJ/kg)	6.8%	75
Budgerigar	maintenance	corn (+ lysine, 3.4 kcal/g, 14.23 MJ/kg)	12%	83
Cockatiel	maintenance	soybeans (+ methionine, 3.5 kcal/g, 14.57 MJ/kg)	11%	68
African grey parrot	maintenance	corn and soybeans; NR	10–15%	84
Rainbow lorikeet	maintenance	egg white (4.0 kcal/g, 16.65 MJ/kg)	2.9%	86
Budgerigar	egg production	corn and soybeans (+ lysine and methionine, 3.2 kcal/g, 13.39 MJ/ kg)	13.2%	89
Budgerigar	growth	soybeans (+ methionine, 3.2 kcal/g, 13.39 MJ/kg)	13.2%	89
Cockatiel	growth	soybeans (+ methionine, 3.5 kcal/g, 14.64 MJ/kg)	20%	90
Cockatiel	growth	purified amino acids (4.0 kcal/g, 16.74 MJ/kg)	0.8% ly- sine	91

^a ME indicates metabolizable energy; + indicates additive; NR, energy concentration not reported.

rainbow lorikeets and observed very low rates of obligatory nitrogen losses. They found that the maintenance protein requirement was only 2.9% when high-quality, readily digestible protein (egg white) was fed. However, the protein in pollen is considerably less digestible,⁵⁷ indicating the need for higher dietary protein levels with this food source.

Protein and amino acid requirements for reproduction are dependent on the number of eggs laid per clutch, the intensity or frequency of egg laying, and the protein composition of the eggs. The amino acid composition of budgerigar eggs is similar to those of chickens⁸⁷ and other avian species,⁸⁸ so there is no reason to expect that the appropriate balance of dietary amino acids should differ markedly among species. However, rates of egg production usually differ between species. Amino acid and protein requirements are increased most in avian species that lay on a daily basis and have large clutches, whereas the requirements for species that lay a single egg or lay on an intermittent cycle are often increased only slightly above maintenance requirements.¹⁵ Budgerigars maintain breeding performance with a 13.2% protein diet (13.39 MJ ME/kg, 0.65% lysine, 0.78% methionine + cysteine) as indicated by number of eggs laid and number of chicks hatched.⁸⁹ A diet of white millet, canary seed, and hulled oats containing 13.4% protein (0.32% lysine, 0.32% methionine + cysteine) but supplemented with vitamins and minerals was inadequate to support reproduction.

In growing birds, dietary protein and amino acids must be supplied for tissue accretion as well as maintenance. The amino acid composition of the tissues of budgerigars is very similar to that of chickens,⁸⁷ indicating that the balance of amino acids required is probably similar to that determined for growing chickens. However, the higher fractional growth rate of psittacine birds because of their altricial mode of development might be expected to increase total amino acid requirements. The requirements for growth are highest at hatch and decrease over time, as the chicks' growth rate begins to slow. The protein requirement for growth of cockatiel chicks is 20% crude protein (CP) (1.0% methionine + cysteine, 1.5% lysine, 14.64 MJ ME/kg) for maximal growth and survivability.⁹⁰ In other experiments,⁹¹ the requirement for lysine to support maximal growth was 0.8% of the dietary dry matter. However, the growth rate of chicks in this experiment was low because of the use of a purified amino acid diet, and the requirement for chicks growing at a normal rate is likely to be higher. Angel and Ballam⁸⁹ found that a corn-soy based diet containing

13.2% protein (0.65% lysine, 0.78% methionine + cysteine, 13.39 MJ ME/kg) supported maximal growth in growing budgerigar chicks. Neither the protein nor the amino acid requirement for growth of other birds in the order Psittaciformes has been determined.

Feathers are a predominant part of the protein mass of birds. In budgerigars and lovebirds, they compose 5.7% and 3.5%, respectively, of the body weight, which is 28% and 22% of total body protein.⁹² Most adult birds molt several times a year. This periodic event is associated with increased amino acid needs for the synthesis of replacement feathers and, to a lesser degree, for the synthesis of new feather follicles, feather sheaths, and epidermal blood vessels. The amino acid composition of feathers is considerably different from other body proteins or egg proteins. Feathers are enriched in cysteine and many of the nonessential amino acids, whereas budgerigar feathers contain only 18% as much lysine and 32% as much methionine as the carcass.⁸⁷ Thus, the primary need for feather growth is cysteine and amino nitrogen. However, whereas feathers grow continuously throughout the day and night, dietary amino acids are supplied only after meals. In the postabsorptive state, most of the amino acids needed for keratin synthesis are mobilized from tissue proteins, although tissue (especially liver) glutathione may supply some of the required cysteine. This diurnal deposition and mobilization of large amounts of tissue proteins markedly decreases the efficiency of amino acid and energy use for molt. It also moderates the balance of dietary amino acids required for molt to more closely resemble the pattern in tissue protein than in feather protein.⁹³ Molt is energetically expensive because of the loss of feather insulation, the cost of synthesizing feather protein, and increased body protein synthesis and degradation. The percentage increase in the energy expenditure associated with molt often exceeds the percentage increase in protein needed for the molt.⁹³ Consequently, molt may not be associated with a change in the dietary amino acid requirement when expressed as percentage of the diet or as mg/kJ. This is because increased food consumption to meet energy requirements results in sufficiently increased amino acid intake to meet requirements for molting.

Nutritionists must be concerned with the quality of dietary protein sources. Protein quality varies on the basis of amino acid balance and digestibility. For example, if 1 protein source contains a lower level of a particular amino acid compared with the bird's requirement (the limiting amino acid), an appropriate complementary protein source, which is

not limiting in that particular amino acid, is often used to meet the bird's requirement. Alternately, purified amino acids can be added to the diet. The digestibility of protein by psittacine birds has not been studied in detail. Given that the assimilation efficiencies of complete diets are similar in psittacine birds (Table 3) and poultry, it is likely that the protein digestibility is generally similar as well. Lorikeets are an exception to this generalization. Digestibility of egg white by rainbow lorikeets is only 13.3%,⁸⁶ presumably because of their small proventriculus and gizzard. Pollen is particularly resistant to digestion by lorikeets but is somewhat better digested by granivorous cockatiels.⁵⁷ Additionally, nestlings have more efficient digestion than adults.

Protein or amino acid deficiency is manifested in reduced growth rates and skeletal muscle deposition.¹⁵ An amino acid imbalance may cause anorexia in addition to aforementioned symptoms. Deficiencies of specific amino acids can produce distinctive pathology. For example, a methionine deficiency during chick growth or molting results in dark, horizontal "stress marks" on feathers.¹¹ Experiments in which specific amino acid deficiencies have been induced have not indicated increased behavioral disorders such as feather picking.¹⁵

A role of high levels of dietary protein in the etiology of renal dysfunction and gout of psittacine birds has occasionally been suggested but is not supported by experimental evidence. Adult male cockatiels fed 20%, 35%, or 70% crude protein for 11 months maintained body weight and general conditioning with no visible signs of protein toxicity.⁶⁸ Neither uric acid precipitates nor articular gout was observed upon postmortem examination regardless of diet. Hepatic and renal enzymes responsible for amino acid catabolism increased in proportion to dietary protein level. However, hepatic sinusoidal and periportal lipogranulomas, which might be indicative of liver damage, were found in birds fed 70% crude protein. These data suggest that levels of crude protein well above expected requirements are tolerated in cockatiels without clinical signs of protein toxicity, and only unrealistically high levels of dietary protein result in mild liver pathology. Although the birds in this study were able to adapt to high-protein diets, such adaptation takes several days in chickens, and therefore gradual changes were made to dietary protein levels to enable this adaptation. Sudden changes from low- to high-protein diets might lead to hyperammonemia, elevated uric acid or urea production, and, potentially, nephritis and gout. On this basis, it is suggested that sudden dietary changes be avoided in

favor of gradual adaptation to new dietary ingredients.

Minerals

Calcium is required in greater quantities than any other mineral and is used for bone mineralization, metabolic homeostasis, and eggshell calcification. In general, the maintenance requirement for calcium is quite small. Although this requirement has not been determined in psittacine birds, the calcium requirement for maintenance in chickens is less than 0.1% of the diet.⁹⁴ Most seeds commonly fed to captive birds have less than 0.1% calcium, and grains (eg, millet, canary seeds, corn) are especially low with less than 0.03% calcium. Experimental⁹⁵ and clinical⁹⁵⁻⁹⁷ evidence supports the contention that diets based exclusively on seeds result in calcium deficiency and that the calcium requirement is above 0.05%. African grey parrots are frequently diagnosed with a hypocalcemia syndrome indicative of calcium deficiency.⁹⁸ However, there is no evidence that these species have higher than normal calcium requirements, and the etiology may be related to an inability to mobilize bone stores during acute periods of dietary inadequacy.

The calcium requirement for growth is expected to be much higher than that of maintenance on the basis of the rapid rate of bone calcification, and requirements will likely be greatest early in life when the fractional growth rate is the highest. Precocial chickens require approximately 1.0% calcium, but experiments examining the calcium requirement of psittacine birds have yet to be published. In chickens, dietary calcium:phosphorus ratios for growth should be maintained between approximately 1.4:1 and 4:1, assuming that vitamin D levels are adequate.⁹⁹ Neither the required level of phosphorus nor its appropriate ratio to calcium is known for psittacine birds, but clinical signs of deficiency have not been widely reported despite the low levels of nonphytate phosphorus in seeds.

Mineralization of the eggshell requires mobilization of calcium from bone; therefore, increased levels of dietary calcium must be supplied before and after reproduction to provide enough calcium for maintenance and/or restoration of bone calcium density. The calcium requirement for egg production, in general, is lower for altricial than precocial species, which lay proportionally larger eggs. In chickens laying an egg a day, the calcium requirement is 3.3% of the diet. In contrast, in cockatiels and budgerigars that lay large clutches, diets containing as little as 0.35% and 0.85% calcium, respectively, supported normal shell calcification.^{66,100}

The availability of calcium and phosphorus in diets can be extremely variable. Calcium and phosphorus found in plants are often less digestible than other sources because of the formation of poorly digestible complexes with phytic and oxalic acid. Calcium is usually low in grains and insects and high in vegetation, although bioavailability is usually low. In the wild, many avian species supplement their diet and that of their chicks with mollusk shells, eggshells, and calciferous grit.¹⁰¹ Some avian species, such as chickens and zebra finches (*Peophila guttata*) have a specific appetite for calcium and will increase their intake of a calcium supplement (eg, oyster shell or cuttlefish bone) when they are laying eggs. It is not known if psittacine birds have a similar capacity to identify and consume calcium-enriched foods and to match this consumption to their requirements.

A calcium deficiency will occur when diets contain too little calcium or vitamin D (essential for calcium homeostasis) or too much phosphorus. Deficiency is manifested in decreased bone mineralization and skeletal abnormalities, particularly in growing birds. For example, in budgerigars, a calcium deficiency causes a demineralization and narrowing of the cortex of the femur.⁹⁵ In chickens, calcium toxicity is less common but results in hypercalcemia and precipitation of calcium urates leading to kidney nephrosis. Also in chickens, signs of phosphorus deficiency and toxicity are similar to those of calcium-deficient birds.¹⁵

Beyond calcium, the requirement of psittacine birds for other minerals is unknown. Zinc toxicity has been reported when very high levels (32 mg/day) were gavaged.¹⁰² Though these high levels have never been reported in natural or commercial diets, they might be achieved if components of poorly galvanized cages are consumed.¹⁰³

Vitamins

Vitamin A is critical for vision, cellular differentiation, immune function, and numerous other parameters.⁸ Vitamin A, like vitamins D, E, and K, is a fat-soluble vitamin, and excretion of this nutrient is much more difficult than for water-soluble vitamins. On this basis, vitamin A toxicities may be quite prevalent in companion bird species, and the incidence of vitamin A deficiency and toxicity is reportedly quite high in captive birds.¹⁰

The vitamin A requirements for psittacine birds are not precisely known, but recent research provides an indication of appropriate dietary levels. In adult female cockatiels, diets containing 2000 or 10,000 IU vitamin A/kg were sufficient for main-

tenance, without signs of deficiency or toxicity. In addition, cockatiels could be maintained on a diet completely devoid of vitamin A (0 IU vitamin A/kg) for 8 months, although immunocompetence was impaired, on the basis of reduction in secondary antibody titers (E. A. K., unpublished data, November 2000). These data suggest that whereas the vitamin A requirement for maintenance is likely to be lower than 2000 IU/kg, this dietary level is sufficient for cockatiel maintenance. In addition, development of vitamin A deficiency in cockatiels at maintenance may require prolonged periods of severely deficient feedstuffs. Vitamin A requirements for other psittacine species remain to be determined.

Symptoms of vitamin A deficiency include keratinization of mucous membranes, anorexia, ruffled plumage, increased susceptibility to infection, and poor conditioning.⁸ In parrots, focal metaplasia of the excretory duct or the glandular epithelium of the salivary glands was identified when liver vitamin A levels reached extremely low levels (<50 IU/g liver).¹⁰⁴ Liver vitamin A levels below 2 IU/g liver were associated with extensive metaplasia of the salivary glands. Symptoms of vitamin A toxicity are very similar, and distinguishing between deficiency and toxicity may require careful assessment of dietary conditions. Interestingly, behavioral changes, specifically changes in vocalization patterns, were observed when cockatiels were fed either deficient or excessive levels of vitamin A.¹⁰⁵ Cockatiels fed 100,000 IU vitamin A/kg diet had increased numbers of vocalizations compared with birds fed 2000 IU/kg (considered to be an adequate level for maintenance), and the peak frequency of vocalizations was reduced. Cockatiels fed 10,000 IU vitamin A/kg or 0 IU vitamin A/kg diet had reduced numbers of vocalizations, and 0 IU resulted in reduced peak amplitude and total power. Although vocalizations may be affected by vitamin A status, it remains to be determined if other nutrients cause a similar change. However, these data suggest that vocalization patterns may be indicative of nutrient status of cockatiels.

Sources of vitamin A in the diet include plant and animal matter. Carotenoids from plants serve as vitamin A precursors for chickens.¹⁰⁶ The capacity of psittacine species to convert carotenoids into vitamin A has not been studied, although on the basis of foods consumed in the wild (plant based), it appears that psittacine species should be quite capable of carotenoid conversion. In foods of animal origin, vitamin A is abundant in the form of retinyl esters, which are considered to be highly available.⁶

Both vitamin A and D toxicosis have been re-

ported in macaws as a result of misuse of liquid vitamin supplementation.^{107,108}

Other nutrients

Psittaciformes, like other avian species, require essential fatty acids, and numerous vitamins and trace minerals in addition to those described above. Unfortunately, research concerning requirements for these nutrients is lacking. Therefore, assumptions must be made based upon poultry literature and knowledge of Psittaciforme physiology when formulating Psittaciforme diets.

The degree to which dietary carotenoids are needed for pigmentation of feathers of Psittaciformes is not well characterized. Efforts to identify carotenoids of dietary origin in the feathers have not been successful¹⁰⁹ and cockatiels can be maintained for over a year on carotenoid-free diets with no loss of feather coloration (E. A. K., unpublished data, August 2000). Furthermore, chicks hatched from these birds develop normal yellow and orange feather colors even when fed carotenoid-free diets.

Captive Diets

The diets consumed by free-living birds can rarely be duplicated in captivity because the vast range of seeds and other food items are not usually available in sufficient quantities. Even if these food items, or very similar ones, could be obtained, they may still not be nutritionally adequate. This is because birds usually eat a quantity of food necessary to satisfy their energy needs, and free-living birds have to expend considerable energy to support thermoregulation, extensive foraging, defenses, etc (see Nutrient Requirements: Energy). Thus, the amount of food consumed by a free-living bird is much greater than the amount of the same foods consumed by that bird in captivity. However, the daily need for amino acids, minerals, and vitamins is relatively constant regardless of energy expenditure. Therefore, birds in captivity must acquire the same daily quantity of essential nutrients as free-living birds but with much less food consumed. Consequently, the concentrations (g/kg) of amino acids, vitamins, and minerals must be higher in captive diets than wild diets, and food items that might be sufficient for a wild bird can be inadequate for the same bird in captivity. Additionally, birds in the wild do not always have the nutritional wisdom to select adequate diets. Many animals are able to balance energy, amino acid, and calcium levels in their diets by selecting among dietary items, but there is little evidence that animals can select for adequate levels of many other nutrients. For example, egg

laying kakapo hens select a diet that apparently is deficient in essential fatty acids even when foods that can meet the requirement are available.¹¹⁰

The nutritional characteristics of food items from domestic plants are often very different from those from native plants. In general, seeds from domestic plants are more concentrated in energy and lower in protein and many other essential nutrients than seeds available in the wild.¹⁵ Likewise, domestic fruits and vegetables are higher in energy and water but lower in other essential nutrients compared with relatives in the wild.¹¹¹ These food items can form the basis of diets for humans when part of a varied diet, but humans grow very slowly and have a very low reproductive output relative to any avian species. Young psittacine chicks double their body weight in a few days—a feat that requires more than a year in humans. Poultry are more similar, though still slower, to psittacine birds in growth rates. Domestic seeds are used as the basis of poultry diets, but they must be heavily fortified with amino acids, vitamins, and minerals to provide nutritionally complete diets.⁶ Both controlled experiments⁵ and clinical experiences^{3,14,112} clearly show that domestic seeds must also be supplemented when used as the basis for diets of psittacine birds. Ullrey et al⁵ compared the nutritional content of seeds commonly used in commercial avian diets with estimated requirements of psittacine birds and concluded that they were typically deficient in amino acids, calcium, available phosphorus, sodium, manganese, zinc, iron, vitamins A, D, K, and B-12, riboflavin, pantothenic acid, choline, and available niacin. Iodine and selenium may be deficient, depending upon the geographical region of production.

Attempts have been made to correct the nutritional balance of domestic seeds by coating them with vitamin and mineral solutions or providing supplement pellets in with the seeds. However, seed coatings are mostly lost when the bird removes the husk, and supplemented pellets are not often consumed. For example, when African grey parrots were presented with a mix of seeds (sunflower, peanuts, safflower), oranges, a variety of vegetables, and a nutritionally complete supplement, they selected a mostly seed diet and consumed only 11% of the dry matter from the supplement.⁵ This self-selected diet was deficient in 12 vitamins, minerals, and amino acids.

Fortification of nutrients through the water is problematic for 2 reasons. First, an aqueous solution of vitamins and minerals is very unstable, and many vitamins are destroyed because of the high redox potential of minerals, especially iron, zinc, and copper. Second, as described above, rates of water con-

sumption are extremely variable among individuals within a species and seasonally, resulting in situations of nutrient deficiencies or excesses.

Another dietary approach is to provide pelleted or extruded mixtures of ingredients that provide all of the required nutrients at levels above the estimated requirements. The processing adheres all of the dietary ingredients together so that the bird cannot select individual components that would result in a nutrient imbalance. This approach has been used very successfully for domestic animals, including poultry, for many decades. It has more recently been applied with success to a variety of psittacine species.^{5,13,112}

Complete diets are usually based on ground grains, such as corn, to supply energy and ground legumes, such as soybean meal or peanut meal, to supply protein. Vitamins, minerals, vegetable oil, and purified amino acids are added in appropriate amounts to make up for deficiencies in the grain and protein sources. In practice, 2 primary criticisms of pelleted diets have been voiced: reluctance of seed-adapted birds to switch to pellets and concern over the lack of variety and enrichment offered by pelleted diets.¹¹² An array of protocols to facilitate conversion has been published in the popular literature. Once birds have been converted to a pelleted diet, the preference of their offspring for seeds is greatly diminished. Dietary enrichment can be accomplished by providing the majority of the nutrition via pellets but also supplying an assortment of fresh fruits and vegetables.¹¹³ Pelleted diets can be formulated so that they complement fruits and vegetables that are offered as part of the diet. This is accomplished by increasing the nonenergy components of the pellets so that the nutrient dilution due to consumption of fruits and vegetables is corrected. Domestic vegetables and especially fruits are predominantly water, so relatively large amounts can be provided without seriously compromising the overall quality of the diet. Ullrey et al⁵ demonstrated the efficacy of providing an extruded complete diet together with fruits and vegetables for 8 different species of breeding psittacine birds (Table 6). In this study, the fledging success was considerably greater when the pelleted diet was fed in place of seeds (90% versus 66%, respectively).

Diets for the Life Cycle

The nutrient requirements and the optimal diet for an animal change throughout the life cycle. Requirements (g/kg diet) are usually highest in the hatchling when growth is rapid and decrease until they reach a minimum after the bird reaches adult

Table 6. Fledging percentage in 8 birds in the order Psittaciformes fed diets based on seeds versus diets based on nutritionally complete extruded pellets.^a

Species	Seeds	Extrusion ^b
Yellow-headed Amazon (<i>Amazona ochrocephala oratrix</i>)	75	100
Forsten's lorikeet (<i>Trichoglossus haematodus forsteni</i>)	62	100
Goldie's lorikeet (<i>Trichoglossus goldiei</i>)	45	83
Blue and gold macaw (<i>Ara ararauna</i>)	62	80
Scarlet macaw (<i>Ara macao</i>)	62	100
Ring-necked parakeet (<i>Psittacula krameri manillensis</i>)	80	100
Rock peplur parakeet (<i>Polytelis anthopeplus</i>)	88	80
Blue-crowned hanging parakeet (<i>Loriculus galgulus</i>)	50	75
Mean	66	90

^a From Ullrey et al.⁵

^b Parents were provided with a mixture of seeds (corn, sunflower, peanuts, safflower) or nutritionally complete extruded pellets. Oranges and vegetables were also provided to both groups.

body weight. Requirements increase for the female a few days prior to egg production and remain elevated until the clutch is laid.¹⁵ Two different diets are often utilized to accommodate these changing needs: a grower-breeder diet and a maintenance diet. A grower-breeder diet that meets the requirements for a growing chick would also likely meet the requirements of the hen for egg production. Consequently, this diet can be introduced at the time birds begin to show nesting behavior and continue to be fed until chicks have fledged. The need for a special diet for periods of molting has yet to be established.

Parents feed their chicks a mixture of food and water. They are apparently very adept at providing the appropriate proportions of food and water and delivering it in the correct amounts and frequencies. At least in crimson rosellas (*Platycercus elegans*), parents are able to discriminate individual chicks and provision them at different rates depending upon their hatching order.¹¹⁴ In many circumstances, hand-feeding of hatchlings is desirable or essential. Special formulated diets based on more water dispersible ingredients facilitate hand feeding. These diets are mixed with appropriate amounts of water and delivered to the back of the chick's mouth. Roudybush and Grau⁹⁰ conducted a series of experiments to determine the appropriate ratio of feed to

water to provide during the growth periods. The ratio that maximized survivability depended upon the age of the chicks. For the first 4 days after hatch, 7% solids and 93% water was optimum, but thereafter 30% solids were needed. Insufficient water during the first few days after hatch results in high mortality, whereas insufficient solids later on results in slow growth rates. Growth rates of hand-fed cockatiels lag somewhat behind those fed by their parents. Presumably this is because parents feed their chicks throughout the night and provide meals more frequently than typical hand-feeding schedules. However, parental provision of nutrients, commensal microflora, or possibly even protective molecules cannot be ruled out.

Conclusion

Formulating or selecting appropriate diets for captive birds in the order Psittaciformes requires knowledge of the birds' wild feeding strategy, digestive anatomy, and physiology and specific knowledge of nutrient requirements in that species or a related species. However, little quantitative data concerning psittacine nutrient requirements have been published. Clearly, much work remains to be done before a complete picture of the nutrient requirements of psittacine birds is elucidated. Results to date indicate that the energy, protein, and calcium requirements are lower in psittacine birds than in poultry during all stages of the life cycle. At this point, little or no research has been conducted on the trace nutrient requirements of psittacine birds, and those established for poultry remain, by default, as the standard. However, there is no compelling evidence that levels of vitamins and trace minerals recommended by the National Research Council for poultry cause either deficiencies or toxicities in psittacine birds. Experimental and clinical evidence demonstrates that diets based on unsupplemented domestic food items are nutritionally incomplete and must be fortified with a variety of amino acids, vitamins, and minerals. The use of pellets formulated to be nutritionally complete as the primary dietary component has proven to be optimal for growth and reproduction of many captive psittacine birds.

References

1. Clements JF. *Birds of the World: A Checklist*. Vista, CA: Ibis Publishing; 2000.
2. Phillips IR. Parrots encountered in practice: a survey of one hundred and twelve cases. *J Small Anim Pract*. 1986;27:189–200.
3. Rosskopf WJ, Woerpel RW. Pet avian conditions and syndromes. In: Rosskopf WJ, Woerpel RW, eds. *Diseases of Cage and Aviary Birds*. Baltimore, MD: Williams and Wilkins; 1996:260–282.
4. Robben JH, Lumeij JT. Comparative studies on parrot foods commercially available in The Netherlands. *Tijdschr Diergeneeskd*. 1989;114:19–25.
5. Ullrey DE, Allen ME, Baer DJ. Formulated diets versus seed mixtures for psittacines. *J Nutr*. 1991;121:S193–S205.
6. NRC. *Nutrient Requirements of Poultry*. Washington, DC: National Academy Press; 1994.
7. Brue RN. Nutrition. In: Ritchie BW, Harrison GJ, Harrison LR, eds. *Avian Medicine: Principles and Application*. Lake Worth, FL: Wingers; 1994:63–95.
8. Lowenstine LJ. Nutritional disorders of birds. In: Fowler ME, ed. *Zoo and Wild Animal Medicine*. Philadelphia, PA: WB Saunders; 1986:201–212.
9. Harrison GJ, Harrison LR. Nutritional diseases. In: Harrison GJ, Harrison LR, eds. *Clinical Avian Medicine and Surgery, Including Aviculture*. Philadelphia, PA: WB Saunders; 1986:717.
10. Bauck L. Nutritional problems in pet birds. *Semin Avian Exotic Pet Med*. 1995;4:3–8.
11. Macwhirter P. Malnutrition. In: Ritchie BW, Harrison GJ, Harrison LR, eds. *Avian Medicine: Principles and Application*. Lake Worth, FL: Wingers; 1994:842–861.
12. Rosskopf WJ, Woerpel RW. Practical feeding strategies for individual pet birds. In: Rosskopf WJ, Woerpel RW, eds. *Diseases of Cage and Aviary Birds*. Baltimore, MD: Williams and Wilkins; 1996:235–241.
13. Roudybush TE. Nutrition of breeding and young psittacine birds: a review. *Isr J Vet Med*. 1996;51:159–160.
14. Schoemaker NJ, Lumeij JT, Dorrestein GM, Beynen AC. Diet-related problems in pet birds. *Tijdschr Diergeneeskd*. 1999;124:39–43.
15. Klasing KC. *Comparative Avian Nutrition*. New York, NY: CAB International; 1998.
16. Morton SR. Granivory in arid regions: comparison of Australia with North and South America. *Ecology (Tempe)*. 1985;66:1859–1866.
17. Morton SR, Davies DH. Food of the zebra finch (*Peophila guttata*) and an examination of granivory in birds of the Australian arid zone. *Aust J Ecol*. 1983;8:235–243.
18. Abramson J, Speer BL, Thomson JB. *The Large Macaws*. Fort Bragg, NC: Raintree; 1995.
19. Long JL, Mawson PR. Diet of regent parrots (*Polytelis anthopeplus*) in the south-west of western Australia. *West Aust Nat*. 1994;19:293–299.
20. Pitter E, Christiansen MB. Ecology, status and conservation of the red-fronted macaw *Ara rubrogenys*. *Bird Conserv Int*. 1995;5:61–78.
21. Trevelyan R. The feeding ecology of Stephen's lory and nectar availability in its food plants. *Biol J Linn Soc*. 1995;56:185–197.
22. Waterhouse RD. Some observations on the ecology of the rainbow lorikeet *Trichoglossus haematodus* in Oatley, south Sydney. *Corella*. 1997;21:17–24.

23. Moorhouse RJ. The diet of the north island kaka (*Nestor meridionalis septentrionalis*) on Kapiti island. *NZ J Ecol.* 1997;21:141–152.
24. Greene TC. Foraging ecology of the red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) and yellow-crowned parakeet (*C. auriceps auriceps*) on Little Barrier Island, Hauraki Gulf, New Zealand. *NZ J Ecol.* 1998;22:161–171.
25. McFarland DC. The biology of the ground parrot, *Pezoporus wallicus*, in Queensland [Australia]: I. Microhabitat use, activity cycle and diet. *Wildl Res.* 1991;18:168–184.
26. Wyndham E. Environment and food of the budgerigar *Melopsittacus undulatus*. *Aust J Ecol.* 1980;5:47–61.
27. Jones D. Feeding ecology of the cockatiel, *Nymphicus hollandicus*, in a grain-growing area. *Aust Wildl Res.* 1987;14:105–115.
28. Chaturvedi N, Almeida MR. Rose-ringed parakeets *Psittacula krameri (scopoli)* feeding on seeds of karvi *Carvia callosa (nees)bremek*. *J Bombay Nat Hist Soc.* 1995;92:121.
29. Oren DC, Novaes FC. Observations on the golden parakeet (*Aratinga guarouba*) in northern Brazil. *Biol Conserv.* 1986;36:329–338.
30. Garnett S, Crowley G. Feeding ecology of hooded parrots *Psephotus dissimilis* during the early wet season. *Emu.* 1995;95:54–61.
31. Trewick S. The diet of kakapo (*Strigops habroptilus*), takahe (*Porphyrio mantelli*) and pukeko (*P. porphyrio melanotus*) studied by faecal analysis. *Notornis.* 1996;43:79–84.
32. Pepper JW, Male TD, Roberts GE. Foraging ecology of the south Australian glossy black-cockatoo (*Calyptorhynchus lathami halmaturinus*). *Aust Ecol.* 2000;25:16–24.
33. Mack AL, Wright DD. The vulturine parrot, *Psittichas fulgidus*, a threatened New Guinea endemic: notes on its biology and conservation. *Bird Conserv Int.* 1998;8:185–194.
34. Johnstone RE, Kirkby T. Food of the forest red-tailed black cockatoo *Calyptorhynchus banksii naso* in south-west western Australia. *West Aust Nat.* 1999;22:167–177.
35. Wermundsen T. Seasonal change in the diet of the pacific parakeet *Aratinga strenua* in Nicaragua. *Ibis.* 1997;139:566–567.
36. Klasing KC. Avian gastrointestinal anatomy and physiology. *Semin Avian Exotic Pet Med.* 1999;8:42–50.
37. Ziswiler V, Farner DS. Digestion and the digestive system. In: Farner DS, King JR, Parkes KC, eds. *Avian Biology*. New York, NY: Academic Press; 1972: 343–430.
38. Guentert M. Morphologische untersuchungen zur adaptiven radiation des verdauungstraktes bei papegeien (psittaci). *Zool Jb Anat.* 1981;106:471–526.
39. Homberger DG, Brush AH. Functional-morphological and biochemical correlations of the keratinized structures in the African gray parrot, *Psittacus erithacus* (Aves). *Zoomorphology (Berl).* 1986;106: 103–114.
40. Churchill DM, Christensen P. Observations on pollen harvesting by brush-tongued lorikeets. *Aust J Zool.* 1970;18:427–437.
41. Homberger D. Functional anatomy of parrot tongues. *J Ornithol.* 1985;126:345–346.
42. Homberger DG. Funktionell-morphologische untersuchungen zur radiation der ernahrungs und trinkmethoden der papageien (psittaci). *Bonner Zool Monogr.* 1980;13:1–187.
43. Richardson KC, Wooller RD. Adaptations of the alimentary tracts of some Australian lorikeets to a diet of pollen and nectar. *Aust J Zool.* 1990;38:581–586.
44. El Boushy AR, Van der Poel AFB, Verhaart JCJ, Kennedy DA. Sensory involvement controls feed intake in poultry. *Feedstuffs.* 1989;61:16–41.
45. Berkhoudt H. Special sense organs: structure and function of the avian taste receptors. In: King AS, McLelland J, eds. *Form and Function in Birds*. New York, NY: Academic Press; 1985:462–496.
46. Jackson S, Nicolson SW, Lotz CN. Sugar preferences and “side bias” in cape sugarbirds and lesser double-collared sunbirds. *Auk.* 1998;115:156–165.
47. Lloyd P. Sucrose concentration preferences of two southern African sunbirds. *Ostrich.* 1989;60:134–135.
48. Hainsworth FR, Wolf LL. Nectar characteristics and food selection by hummingbirds. *Oecologia.* 1976; 25:101–113.
49. Buchsbaum R, Valiela I, Swain T. The role of phenolic compounds and other plant constituents in feeding by Canada geese in a coastal marsh. *Oecologia (Berl).* 1984;63:343–349.
50. Yang XJ, Wen XJ, Wang SZ, et al. The feeding activity of Derby’s parakeet (*Psittacula derbiana*) in captivity. *Zool Res.* 2000;21:115–120.
51. Matson KD, Millam JR, Klasing KC. Taste threshold determination and side-preference in captive cockatiels (*Nymphicus hollandicus*). *Appl Anim Behav Sci.* 2000;69:313–326.
52. Matson KD, Millam JR, Klasing KC. Thresholds for sweet, salt, and sour taste stimuli in cockatiels (*Nymphicus hollandicus*). *Zoo Biol.* 2001;20:1–13.
53. Harriman AE. Laughing gulls offered saline in preference and survival tests. *Physiol Zool.* 1967;40:273–279.
54. Harriman AE, Kare MR. Aversion to saline solutions in starlings, purple grackles, and herring gulls. *Physiol Zool.* 1966;39:123–126.
55. Herness MS, Gilbertson TA. Cellular mechanisms of taste transduction. *Ann Rev Physiol.* 1999;61:873–900.
56. Bartels T, Boos A, Flachsbarth MF, Wolf P. Histological aspects of the digestive system of the budgerigar. *First Int Symp Pet Bird Nutr.* 1997;26.
57. Brice AT, Dahl KH, Grau CR. Pollen digestibility by hummingbirds and psittacines. *Condor.* 1989;91: 681–688.
58. Wolf P, Kamphues J, Bartels T, Dehning S. Enzymes

- activities along the intestinal tract of pet birds. *First Int Symp Pet Bird Nutr.* 1997;28.
59. Clench MH, Mathias JR. The avian cecum—a review. *Wilson Bull.* 1995;107:93–121.
 60. Karasov WH, Cork SJ. Test of a reactor-based digestion optimization model for nectar-eating rainbow lorikeets. *Physiol Zool.* 1996;69:117–138.
 61. Karasov WH. Digestion in birds: chemical and physiological determinants and ecological implications. *Stud Avian Biol.* 1990;13:391–415.
 62. Sakurai F, Hamamatsu M, Takahashi R, et al. Endogenous amino acids in budgerigars (*Melopsittacus undulatus*). *Exp Anim (Tokyo).* 1998;47:189–194.
 63. Macmillen RE. Water economy of granivorous birds: a predictive model. *Condor.* 1990;92:379–392.
 64. MacMillen RE, Baudinette RV. Water economy of granivorous birds: Australian parrots. *Funct Ecol.* 1993;7:704–712.
 65. Weathers WW, Caccamise DF. Temperature regulation and water requirements of the monk parakeet, *Myiopsitta monachus*. *Oecologia.* 1975;18:328–342.
 66. Earle KE, Clarke NR. The nutrition of the budgerigar (*Melopsittacus undulatus*). *J Nutr.* 1991;121:186S–192S.
 67. Lumeij JT, Westerhof L. The use of the water deprivation test for the diagnosis of apparent psychogenic polydipsia in a socially deprived African gray parrot (*Psittacus erithacus erithacus*). *Avian Pathol.* 1988;17:875–878.
 68. Koutsos EA, Smith J, Woods L, Klasing KC. Adult cockatiels (*Nymphicus hollandicus*) undergo metabolic adaptation to high protein diets. *J Nutr.* 2001;137:2014–2020.
 69. Wolf P, Kamphues J. Water intake of pet birds—basic data and influencing factors. *First Int Symp Pet Bird Nutr.* 1997;74.
 70. McNab BK, Salisbury CA. Energetics of New Zealand's temperate parrots. *NZ J Zool.* 1995;22:339–349.
 71. Buttemer WA, Hayworth AM, Weathers WW, Nagy KA. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol Zool.* 1986;59:131–149.
 72. Tucker VA. The energetics of bird flight. *Sci Am.* 1969;220:70–78.
 73. Williams JB, Withers PC, Bradshaw SD, Nagy KA. Metabolism and water flux of captive and free-living Australian parrots. *Aust J Zool.* 1991;39:131–142.
 74. Pearson JT. Development of thermoregulation and posthatching growth in the altricial cockatiel *Nymphicus hollandicus*. *Phys Zool.* 1998;71:237–244.
 75. Kamphues J, Wolf P. Energy and nutrient requirements of growing canaries, budgerigars, and lovebirds. *First Int Symp Pet Bird Nutr.* 1997;80.
 76. Daan S, Masman D, Groenewold A. Avian basal metabolic rates—their association with body composition and energy expenditure in nature. *Am J Physiol.* 1990;259:R333–R340.
 77. Nagy KA. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol Monogr.* 1987;57:111–128.
 78. Downs CT. Ingestion patterns and daily energy intake on a sugary diet: the red lory *Eos bornea* and the malachite sunbird *Nectarinia famosa*. *Ibis.* 2000;142:359–364.
 79. Drepper K, Menke K, Schulze G, Wachter-vormann U. Untersuchungen zum protein- und energiebedarf adulter welesittche (*Melopsittacus undulatus*). *Klein-tierpraxis.* 1988;33.
 80. Austic RE. Nutritional and metabolic interrelationships of arginine, glutamic acid and proline in the chick. *Fed Proc.* 1976;35:1914–1916.
 81. Taylor EJ, Nott HMR, Earle KE. Dietary glycine: its importance in growth and development of the budgerigar (*Melopsittacus undulatus*). *J Nutr.* 1994;124:2555S–2558S.
 82. Sailaja R, Kotak VC, Sharp PJ, et al. Environmental, dietary, and hormonal factors in the regulation of seasonal breeding in free-living female Indian rose-ringed parakeets (*Psittacula krameri*). *Horm Behav.* 1988;22:518–527.
 83. Underwood MS, Polin D, O'Handley P, Wiggers P. Short term energy and protein utilization by budgerigars fed isocaloric diets of varying protein concentrations. *Proc Annu Conf Assoc Avian Vet.* 1991;227–237.
 84. Kamphues J, Otte W, Wolf P. Effects of increasing protein intake on various parameters of nitrogen metabolism in grey parrots (*Psittacus erithacus erithacus*). In: Kamphues J, Wolf P, Rabehl N, eds. *First Int Symp Pet Bird Nutr.* 1997;118.
 85. Pryor GS. Comparative protein requirements and digestive strategies of three species of parrots with distinct dietary specializations. *Am Zool.* 1999;39:93A.
 86. Frankel TL, Avram DS. Protein requirements of rainbow lorikeets, *Trichoglossus haematodus*. *Aust J Zool.* 2001;49:435–443.
 87. Massey DM, Sellwood EHB. The amino-acid composition of budgerigar diet, tissues and carcass. *Vet Rec.* 1960;72:283–287.
 88. Murphy ME. Amino acid compositions of avian eggs and tissues—nutritional implications. *J Avian Biol.* 1994;25:27–38.
 89. Angel R, Ballam G. Dietary effect on parakeet plasma uric acid, reproduction and growth. *Proc Annu Conf Assoc Avian Vet.* 1995;27–32.
 90. Roudybush TE, Grau CR. Food and water interrelations and the protein requirement for growth of an altricial bird, the cockatiel (*Nymphicus hollandicus*). *J Nutr.* 1986;116:552–559.
 91. Roudybush TE, Grau CR. Lysine requirements of cockatiel chicks. *Proc 34th West Poult Dis Conf.* 1985;34:113–115.
 92. Kamphues J, Wolf P, Rabehl N. Development of body composition in growing pet birds (canaries, budgerigars, and lovebirds). In: Kamphues J, Wolf P, Rabehl N, eds. *First Int Symp Pet Bird Nutr.* 1997;38.
 93. Murphy ME. Energetics and nutrition of molt. In:

- Carey C, ed. *Avian Energetics and Nutritional Ecology*. New York, NY: Chapman & Hall; 1996:158–198.
94. Rowland LO, Sloain DR, Fry JL, Harmes RH. Calcium requirement for bone maintenance of aged non-laying hens. *Poult Sci*. 1973;52:1415–1418.
 95. Arnold SA, Kram MA, Hintz HF, et al. Nutritional secondary hyperparathyroidism in the parakeet. *Cornell Vet*. 1973;64:37–46.
 96. Randall MG. Nutritionally induced hypocalcemic tetany in an Amazon parrot. *J Am Vet Med Assoc*. 1981;179:1277–1278.
 97. Wallach JD, Flieg GM. Nutritional secondary hyperparathyroidism in captive psittacine birds. *J Am Vet Med Assoc*. 1967;151:880–883.
 98. Roskopf WJ, Woerpel RW, Lane RA. The hypocalcemia syndrome in African greys: an updated clinical viewpoint with current recommendations for treatment. *Proc Annu Conf Assoc Avian Vet*. 1985;129–131.
 99. Shafey TM. Calcium tolerance of growing chickens—effect of ratio of dietary calcium to available phosphorus. *Worlds Poult Sci J*. 1993;49:5–18.
 100. Roudybush T. *Nutrition*. In: Roskopf W, Woerpel R, eds. *Diseases of Cage and Aviary Birds*. Baltimore, MD: Williams & Wilkins; 1996:218–234.
 101. Graveland J. Avian eggshell formation in calcium-rich and calcium-poor habitats—importance of snail shells and anthropogenic calcium sources. *Can J Zool—Rev Can Zool*. 1996;74:1035–1044.
 102. Howard BR. Health risks of housing small psittacines in galvanized wire mesh cages. *J Am Vet Med Assoc*. 1992;200:1667–1674.
 103. Reece RL, Dickson DB, Burrowes PJ. Zinc toxicity new wire disease in aviary birds. *Aust Vet J*. 1986;63:199.
 104. Dorrestein GM, Zwart S, van der Hage MH, Schrijver J. Metaplastic alterations in the salivary glands of parrots in relation to liver vitamin A levels. *Proc Int Conf Zoo Avian Med*. 1987;69–74.
 105. Koutsos EA, Pham HN, Millam JR, Klasing KC. Vocalizations of cockatiels (*Nymphicus hollandicus*) are affected by dietary vitamin A concentration. *Proc 35th Int Congr Int Soc Appl Ethol*. 2001;116.
 106. Thompson SY, Ganguly J, Kon SK. The conversion of β -carotene to vitamin A in the intestine. 1949;3:50–781.
 107. Takeshita K, Graham DL, Silverman S. Hypervitaminosis D in baby macaws. *AAV Proc Int Conf Avian Med*. 1986;341–344.
 108. Schoemaker NJ, Lumeij JT, Beynen AC. Polyuria and polydipsia due to vitamin and mineral oversupplementation of the diet of a salmon crested cockatoo (*Cacatua moluccensis*) and a blue and gold macaw (*Ara ararauna*). *Avian Pathol*. 1997;26:201–209.
 109. Stradi R. *The colour of flight: carotenoids in bird plumage*. Milan, Italy: Solei Gruppo Editoriale Informatico; 1998.
 110. Body DR, Powlesland RG. Lipid composition of a clutch of kakapo (*Strigops habroptilus*) (Aves: Caccatuidae) eggs. *NZ J Zool*. 1990;17:341–346.
 111. Bosque C, Pacheco MA. Dietary nitrogen as a limiting nutrient in frugivorous birds. *Rev Chil Hist Nat*. 2000;73:441–450.
 112. Lumeij JT, Zijp MNM, Schippers R. The acceptance of a recently introduced extruded parrot food in The Netherlands. *Isr J Vet Med*. 1996;51:161–164.
 113. Field DA, Thomas R. Environmental enrichment for psittacines at Edinburgh zoo. *Int Zoo Yearb*. 2000;37:232–237.
 114. Krebs EA, Cunningham RB, Donnelly CF. Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. *Anim Behav*. 1999;57:753–763.
 115. Toyne EP, Flanagan JNM. Observations on the breeding, diet and behaviour of the red-faced parrot *Hapalopsittaca pyrrhops* in southern Ecuador. *Bull Br Ornithol Club*. 1997;117:257–263.
 116. Galetti M. Diet of the scaly-headed parrot (*Pionus maximiliani*) in a semideciduous forest in south-eastern Brazil. *Biotropica*. 1993;25:419–425.
 117. Bonadie WA, Bacon PR. Year-round utilisation of fragmented palm swamp forest by red-bellied macaws (*Ara manilata*) and orange-winged parrots (*Amazona amazonica*) in the Nariva swamp (Trinidad). *Biol Conserv*. 2000;95:1–5.
 118. Rowley I, Russell E, Palmer M. The food preference of cockatoos: an aviary experiment. *Aust Wildl Res*. 1989;16:19–32.
 119. King CE, Heinhuis H, Brouwer K. Management and husbandry of black cockatoos *Calyptorhynchus* spp. in captivity. *Int Zoo Yearb*. 2000;37:87–116.
 120. Cannon CE. Observations on the food and energy requirements of rainbow lorikeets, *Trichoglossus haematodus*. *Aust Wildl Res*. 1979;6:337–346.
 121. Saini HK, Dhindsa MS. Food preferences of captive rose-ringed parakeets: a comparison of two methods. *Jpn J Ornithol*. 1993;41:39–45.
 122. Taylor MR. Natural history, behaviour and captive management of the palm cockatoo *Probosciger aterrimus* in North America. *Int Zoo Yearb*. 2000;37:61–69.
 123. Smith GT, Moore LA. Foods of corellas *Cacatua pastinator* in western Australia. *Emu*. 1991;91:87–92.
 124. Temby ID, Emison WB. Foods of the long-billed corella (*Cacatua tenuirostris*). *Aust Wildl Res*. 1986;13:57–64.
 125. Cannon CE. The diet of eastern and pale-headed rosellas. *Emu*. 1981;81:101–110.
 126. Martuscelli P. Ecology and conservation of the red-tailed Amazon *Amazona brasiliensis* in south-eastern Brazil. *Bird Conserv Int*. 1995;5:405–420.
 127. Elliott GP, Dilks PJ, O'Donnell CFJ. The ecology of yellow-crowned parakeets (*Cyanoramphus auriceps*) in nothofagus forest in Fiordland, New Zealand. *NZ J Zool*. 1996;23:249–265.
 128. McNab BK. Food habits and the basal rate of me-

- tabolism in birds. *Oecologia (Berl)*. 1988;77:343–349.
129. Beggs JR, Wilson PR. Energetics of south island kaka *Nestor-meridionalis-meridionalis* feeding on the larvae of kanuka longhorn beetles *Ochrocydus-huttoni*. *NZ J Ecol*. 1987;10:143–148.
130. Kasuya K, Karakida T, Okawara Y, Kobayashi H. Comparative studies of food intake and water balance following water deprivation in the budgerigar (*Melopsittacus undulatus*) and Japanese quail (*Coturnix coturnix japonica*). *J Yamashina Inst Ornithol*. 1987;19:89–102.