

## From blackbirds and thrushes . . . to the gut-loaded cricket: a new approach to zoo animal nutrition

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Zoo animal nutritionists need to make decisions about diet composition for a wide variety of vertebrate species, including those with very specialized diets (dietary specialists). For some zoo species it is common to refer to the published literature on the nutrient requirements of analogous domestic animals, such as cattle, horses and cats, as well as human beings (Allen & Oftedal, 1996). When this information is combined with knowledge of natural history, feeding patterns, composition of foods consumed in the wild and gastrointestinal tract morphology, it is possible to develop a sound foundation for a successful feeding programme for many zoo animals.

Dietary specialists with rigid feeding habits present a more difficult challenge. There are no analogous domestic species with which to compare obligate filter-feeders such as flamingos, obligate fish-eaters such as seals, and obligate insect-eaters such as insectivorous bats. For these and other dietary specialists, the peculiarities of the consumed foods may have led to the evolution of specific digestive or metabolic adaptations. It may be necessary to make species-specific dietary adjustments. For example, flamingos require the addition of carotenoids to grain-based captive diets to assure normal feather pigmentation (Fox, 1975). Nutritional myopathies in seals and sea lions can be avoided by the addition of vitamin E to their diets of frozen, thawed fish; this replaces the oxidized vitamin E lost during storage (Oftedal & Boness, 1983; Citino *et al.* 1985). Rickets and osteomalacia can be prevented in insectivorous lizards by providing Ca-enriched insects (Allen & Oftedal, 1994).

### DR WIDDOWSON'S WORK

A novel solution to enriching insects with Ca was suggested by Dr Elsie Widdowson. Dr Widdowson was first introduced to me in 1981 at Addenbrooke's Hospital. I knew of her mainly due to her work with the food composition tables, for as a nutritionist with the Brookfield Zoo (Chicago Zoological Society), I relied heavily on the McCance and Widdowson tables (Paul & Southgate, 1978) in formulating and balancing diets for many zoo animals. I was also aware of her work with body composition, neonates and gastrointestinal tract development (Spray & Widdowson, 1950; Widdowson *et al.* 1976). What I had not realized until that meeting was that Dr Widdowson had been involved in studies with Dr Lorette Bilby which resulted in a *British Journal of Nutrition* paper on blackbirds and thrushes (Bilby & Widdowson, 1971). At our meeting Dr Widdowson expressed great interest about the common zoo problem of Ca deficiency in captive insectivorous species. Rickets and osteomalacia were common in zoo animals exclusively fed on mealworm larvae, waxmoth larvae and crickets, insects commonly used for insect-eating animals in the US. It seemed improbable to me that wild animals developed Ca deficiencies from consuming insects and other invertebrates. To my surprise and pleasure,

Dr Widdowson related the story of her research with blackbirds and thrushes. Dr Widdowson, I realized, knew no bounds with respect to areas of scientific investigation. She later ventured into comparative studies with bears and seals (Oftedal *et al.* 1989, 1993).

*The problem: invertebrates as food*

The bony skeleton in vertebrates contains over 98% of the Ca in the body (Spray & Widdowson, 1950). Since invertebrate species lack an internal bony skeleton, Ca concentrations are low in many insects (Table 1). The cuticle (exoskeleton) of invertebrates contains chitin, a polymer of N-acetylglucosamine, which is similar in its structure to cellulose. Chitin provides structural support to the cuticle. The outermost layer of the cuticle consists of sclerotized (tanned) chitin which is rigid and helps protect softer tissues within the body. Some terrestrial and/or aquatic invertebrates, such as decapods, have calcified cuticles, whereas most insects do not. The crickets, mealworm larvae, waxworm larvae and grasshoppers used in zoos are poor sources of Ca (0.3–1.8 g Ca/kg DM). Rickets and osteomalacia often result when these invertebrates are fed to vertebrates as the sole food without Ca supplementation.

How then do vertebrates that specialize in, and depend on, invertebrates as food obtain sufficient Ca to maintain health? This question intrigued Dr Widdowson, who set out with Dr Lorette Bilby to study insectivorous blackbirds (*Turdus merula*) and thrushes (*Turdus philomelos*) that were known to consume earthworms, caterpillars and adult insects. They intended: 'to find out how they [birds] obtain from these unpromising foods sufficient calcium for their needs' (Bilby & Widdowson, 1971). The birds were weighed when newly hatched and again at day 13 (blackbird) or day 12 (thrush). Body mass increased dramatically in both species. The blackbirds, by day 13, had increased their hatching mass by fourteen times and the thrushes by day 12 had increased their mass by ten times.

Total Ca accretion in the bodies of these birds was remarkable, representing an increase of 80–100-fold (Fig. 1). The relatively poorly calcified bone of the hatchling became well mineralized in a period of 12–13 d. From hatching to 4–5 d, the increase of Ca was slow but at 12–13 d the fledgling femurs reached a stage of calcification similar to those of newborn infants, 21-d-old rats and 17-d-old chickens. Of particular interest was the observation that at 1–2 d the Ca in the guts of the blackbirds (*n* 4) was equivalent to 36% of that in their bodies, while in the thrushes (*n* 3) Ca in the digestive tract was 42% of that in their bodies, suggesting that a high-Ca food was being ingested.

Table 1. *Calcium content and calcium : phosphorus ratio of invertebrates*

Invertebrate*	Ca content (g/kg)	Ca : P
Earthworm	11.8	1.31 : 1
Mosquito	8.2	0.66 : 1
Cockroach	5.7	0.74 : 1
Termite	3.4	0.60 : 1
Cricket	1.8	0.21 : 1
Mayfly	1.7	0.15 : 1
Waxmoth larvae	0.3	0.08 : 1

\* Earthworm, *Lumbricus* sp.; mosquito, *Culex* sp.; cockroach, *Periplaneta americana*; termite, *Hodotermes mossambicus*; cricket, *Acheta domestica*; mayfly, order *Ephemeroptera*; waxmoth larvae, *Galleria mellonella*. (From Allen, 1989b.)

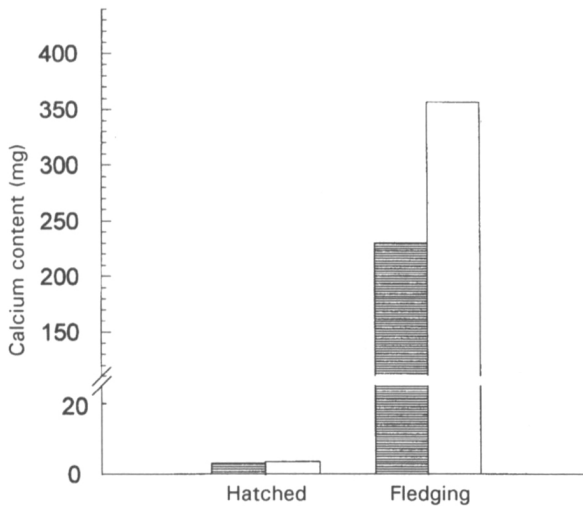


Fig. 1. Calcium content of the empty bodies of nestling thrushes (*Turdus philomelos*; ▨) and blackbirds (*Turdus merula*; □) when recently hatched and at the time of fledging (12–13 d of age). (Data from Bilby & Widdowson, 1971.)

These altricial birds obviously gained both mass and Ca at rapid rates. Since earthworms appeared to be the primary food offered by parents to young, earthworms were collected near Cambridge. They were found to contain a mean of 8.9 g Ca/kg. Gut contents contained 16.6 g Ca/kg and the earthworm body, 2.3 g Ca/kg. The Ca provided by earthworms was also calculated. Small worms weighed 0.3 g and large worms, 1.3 g. The authors calculated that if the birds absorbed and retained all Ca, blackbirds would need to consume thirty large or 130 small worms, and thrushes would need to consume twenty large or eighty-five small worms to obtain sufficient Ca for their needs. The authors concluded: 'it seems likely that it is the gut contents of these invertebrates that provide the nestling birds with most of the calcium they need. How the birds fare in an area where the soil is not chalky still remains to be discovered.'

#### CALCIUM AND VITAMIN D STATUS OF CAPTIVE INSECTIVOROUS ANIMALS

The Bilby and Widdowson work provided an excellent model for the problem faced by insect- or invertebrate-eating animals. In zoos, insects had sometimes been coated with Ca by 'dusting' insects with a powdered supplement. However, the powder does not adhere well to some insects (e.g. *Tenebrio* larvae), and crickets quickly groom the dust from their bodies. Based on the Bilby & Widdowson (1971) study, a method of internal supplementation ('gut-loading') was tested with crickets. Crickets were fed on manufactured, powdered diets ranging from 20 to 120 g Ca/kg (Allen & Oftedal, 1989). The Ca content of the crickets increased progressively with an increase in dietary Ca (Fig. 2(a)), with the result that crickets consuming diets containing 80–120 g Ca/kg had a Ca : P ratio greater than 1 : 1. P concentrations did not change and remained at approximately 8 g P/kg (Fig. 2(b)). Radiography demonstrated that Ca accumulated in the gut rather than in the bodies (Fig. 3).

In a series of experiments with a nocturnal lizard, the leopard gecko (*Eublepharis macularius*), the effects on bone composition and bone integrity were studied by

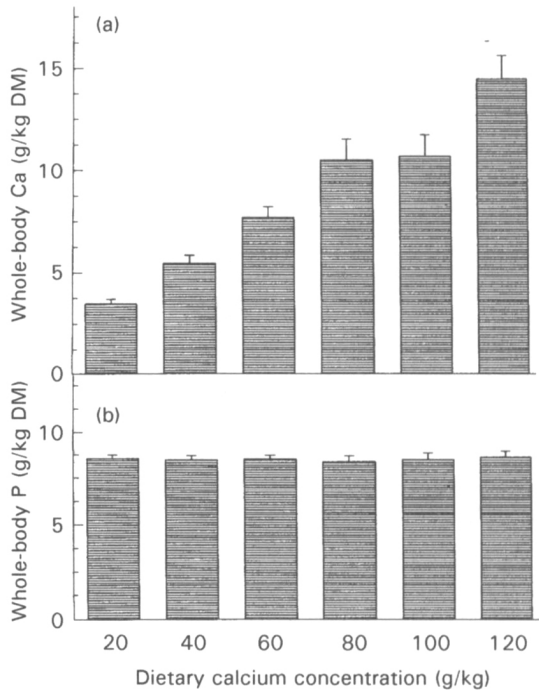


Fig. 2. The effect of dietary calcium concentration on (a) calcium and (b) phosphorus concentrations of the whole body (including digestive tract contents) of house crickets (*Acheta domestica*). Crickets were fed on the diets for 48–120 h before being assayed for calcium by atomic absorption spectroscopy and for phosphorus by the molybdo-vanadate method. Values are means with their standard errors represented by vertical bars. (From Allen & Oftedal, 1989.)

manipulating the Ca content of crickets. Growth rate, feed intake, bone ash content and bone Ca content were greater in juvenile leopard geckos fed on high-Ca crickets than they were in geckos fed on low-Ca crickets (Allen, 1989b). Radiographs demonstrated that geckos fed on high-Ca crickets had well-mineralized bone at the end of 8 months, but low-Ca-fed geckos had poorly mineralized bone with fractures and thin cortices (Fig. 4). Periosteal proliferation and unmineralized, retained cartilage were observed histologically in the low-Ca-fed geckos. The high-Ca-fed geckos had well mineralized cortices and good progression from cartilage to bone (Allen, 1989a). Cholecalciferol concentration of crickets was also manipulated and had an effect on bone Ca concentration independent of dietary Ca (Allen, 1989b).

#### WHAT IS THE OPTIMAL LEVEL FOR DIETARY SUPPLEMENTATION?

Although the general consensus among herpetologists is that crickets and other insects should be supplemented with Ca, the optimal dietary Ca level for insectivorous reptiles is unknown. A 3-month Ca balance trial was conducted to define the dietary Ca requirement of young leopard geckos (Allen, 1989b). Geckos were initially depleted of Ca by feeding unsupplemented (with Ca) crickets for 2 months, and were then fed on crickets maintained for at least 48 h on diets of 20, 40, 60 and 80 g Ca/kg, resulting in Ca levels ranging from 2.7 to 8.5 g/kg in the insects. On all dietary treatments, the leopard geckos retained a very high proportion of ingested Ca (95%) during the first 2 months. In the third month,

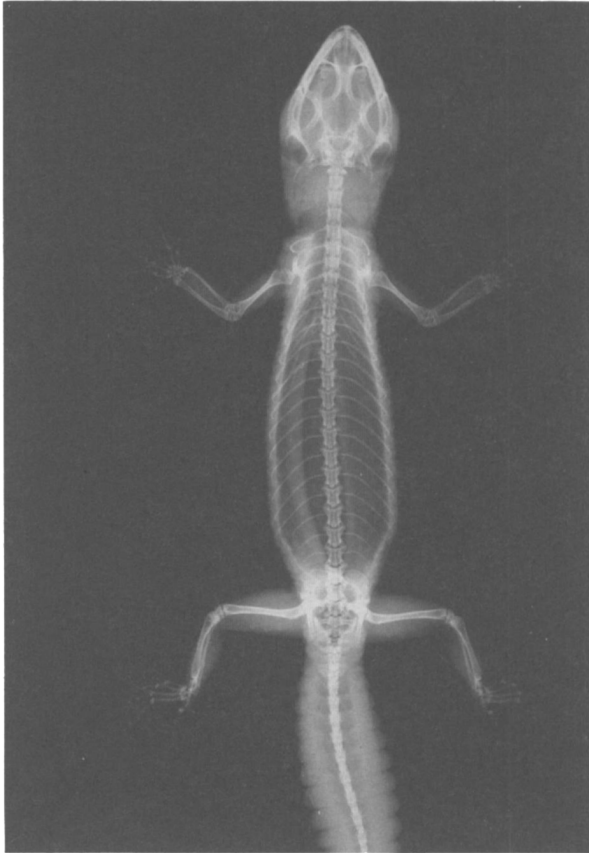


Fig. 3. Radiograph of house crickets (*Acheta domestica*) demonstrating calcium accumulation in the digestive tract. The crickets were fed on diets containing 80 g Ca/kg for at least 48 h. (From Allen & Oftedal, 1989.)

retention dropped dramatically to as low as 16 % among geckos on high-Ca crickets (8.5 g Ca/kg), indicating repletion of body Ca stores, while geckos on the lower Ca crickets (2.7–6.1 g Ca/kg) continued to retain high proportions of Ca (Fig. 5). It appears that leopard geckos require no more than 8.5 g Ca/kg (Ca : P ratio 0.9 : 1) for growth. Zoos in the US now commonly supplement crickets and mealworm larvae by feeding them on high-Ca diets at least 48 h before feeding them to insectivorous lizards.

A similar experiment was conducted with a diurnal (basking) gecko, the Madagascar giant day gecko (*Phelsuma madagascariensis*). These juvenile geckos experienced high mortality and bone demineralization when maintained on the same diets as the leopard geckos, suggesting that the day gecko may have different nutritional requirements (Allen, 1989a). The failure of the day gecko to thrive, in spite of adequate dietary Ca, suggested that additional vitamin D or ultraviolet light B (UVB) might be important. Day geckos and other basking lizards normally rely on the sun to provide heat for thermoregulation. Do basking lizards also depend on the sun, rather than on a dietary source, to satisfy their requirements for cholecalciferol?

Subsequent work with vitamin D and Ca in the herbivorous green iguana (*Iguana iguana*), a New World basking lizard, has shown that even when fed on diets with adequate Ca and high concentrations of cholecalciferol (75 µg/kg diet DM), iguanas developed low circulating levels of 25-hydroxycholecalciferol and bone demineralization; in some cases iguanas died (Richman *et al.* 1995; Allen *et al.* 1996). However, vitamin D-deficient iguanas responded positively to exposure to UVB radiation with marked increases in concentrations of circulating 25-hydroxycholecalciferol (Bernard *et al.* 1991; Bernard,



(a)

Fig. 4. Radiographs of juvenile leopard geckos (*Eublepharis macularius*) that had been fed on crickets that were either (a) high (8.6 g/kg) or (b) low (2.0 g/kg) in calcium for 8 months. Compare the well-mineralized skeleton in (a) with the poorly mineralized skeleton, including thin cortices and fractures of long bones, in (b). Gecko carcasses were eviscerated before radiography. (From Allen, 1989b.)

1995). Recently, studies with the rare, captive Komodo dragon (*Varanus komodoensis*) have demonstrated that this carnivorous lizard responds to both exposure to the sun and to artificial sources of UVB with increasing concentrations of circulating 25-hydroxycholecalciferol (M. E. Allen, M. Bush, O. T. Oftedal, R. Rosscoe, T. Walsh and M. F. Holick, unpublished results).

#### CONCLUSIONS

For vertebrates that do eat worms or other soil-dwelling invertebrates, Ca intake may be adequate, as Bilby & Widdowson (1971) noted. The larger issue, however, still remains: how do bats, swallows and other vertebrates, that depend primarily on flying insects, obtain sufficient Ca (Barclay, 1995)? One possible explanation is that behavioural mechanisms are in place that result in the seeking-out of Ca-rich substances, particularly during reproductive phases. In the US, purple martins (*Progne subis*) are reported to seek and obtain egg shells (placed in platform feeders) and offer them to their fledgling offspring (E. Morton, National Zoological Park, unpublished results). This area of research deserves





(b)

Fig. 4. (continued)

further investigation. The initial research by Drs Bilby and Widdowson inspired studies in insectivorous animals of Ca requirements, bone composition differences, and pathology related to dietary Ca. This, in turn, has stimulated research in vitamin D requirements of zoo animals, specifically lizards. The relationship between UVB, vitamin D and Ca in zoo animals is an exciting area in which relatively little is known about species differences. If the propagation of captive animals in zoos is to succeed, such information is critical.

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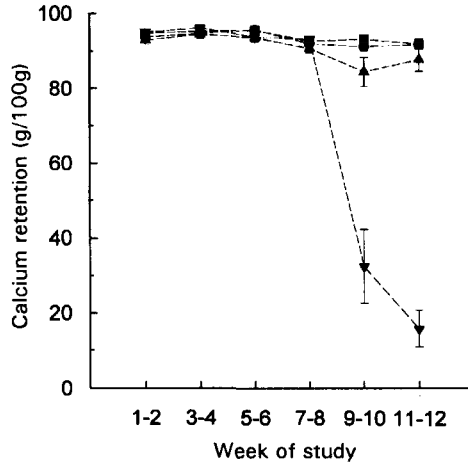


Fig. 5. Retention of calcium by leopard geckos (*Eublepharis macularius*) consuming crickets maintained on diets containing 20 (●), 40 (■), 60 (▲), or 80 (▼) g calcium/kg. Each point represents the mean of five or six geckos for a 2-week period; standard errors are represented by vertical bars. Retention is expressed as g calcium per 100 g dietary calcium. (From Allen, 1989b.)

manuscript. Dr Margaret Ashwell kindly invited my participation in this memorable event in the honour of Dr Widdowson. I would like to offer a special thanks to Dr Widdowson for her inspiration and guidance to biological scientists around the world.

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