Physiology

(A. Gastrointestinal

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DAVID C. HOUSTON Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences University of Glasgow, Glasgow G12 8QQ, United Kingdom

GARY E. DUKE

Department of Veterinary Pathobiology, College of Veterinary Medicine, University of Minnesota, St. Paul, MN 55126 U.S.A

GASTROINTESTINAL PHYSIOLOGY AND NUTRITION

Most studies of nutrition and gastrointestinal (aka GI) physiology in birds have been conducted on domestic fowl. Birds of prey provide an interesting contrast to domestic fowl because of their carnivorous diets. This part of Chapter 16 summarizes our knowledge of anatomy, gastric secretion and motility, pellet formation and egestion, and the techniques available to study these aspects of raptor biology.

Gastrointestinal Physiology

Anatomical considerations. It is useful to have some notion of anatomy in order to better understand function. The GI tracts of raptors differ significantly from those of domestic fowl, with which most biologists are familiar (Fig.1; Duke 1978). Whereas turkeys have a well-developed crop, that of many raptors is poorly

developed, and owls have no crop at all, only a simple enlargement of the esophagus. The crop is largely a food-storage area with little secretory activity, and is exceptionally well developed only in some vultures, whose crop allows them to consume up to 20% of their body weight in a single meal (Houston 1976). The stomach of turkeys, and virtually all other avian species except raptors and Ardeidae, consists of two pairs of alternately contracting muscles that grind food. The meat diet of raptors does not require strong mechanical grinding, and birds of prey have a simpler muscular stomach in which acid secretion and enzyme action start to break down the food. Digestion is continued in the small intestine, which also is the site of absorption. The pancreas fills the entire duodenal loop in turkeys, but occupies only half of the loop in owls, and is even smaller in hawks. There seems to be considerable variation in the total length of the small intestine between species of both raptors and owls. After correction for body-size differences, species such as falcons, which use a method of prey capture that requires extreme acceleration in flight, have a small intestine length about 50% shorter than that found in species such as eagles, buzzards, and kites that have less need for speed and agility when hunting (Barton and Houston 1994a). This may be an adaptation to reduce the overall weight of the digestive tract in those species which have an extremely active hunting strategy, and it does have the consequence of giving such species a reduced digestive efficiency and restricted prev selection (see later). Ceca in birds are highly variable in size, and usually are only conspicuous in certain plant-eating birds, where they are the sites of microbial fermentation of plant-cell walls that cannot otherwise be digested (Klasing 1998). Thus, it is not surprising that they are absent in hawks. They are, however, well developed in owls (Fig. 1). It is not clear why Great Horned Owls (*Bubo virginianus*), which eat almost the same diet as Red-tailed Hawks (*Buteo jamaicensis*), have such a different cecal morphology. Perhaps because owls generally swallow their prey whole, the ceca are used to break down the plant material found in the gut contents of their prey. Cecal droppings of owls are readily distinguished from rectal excreta. In Great Horned Owls on a mouse diet, these droppings occur about once every three days (G. Duke, unpubl. data). This information might be used to determine how long an owl has been roosting at a particular site.

Gastric secretions and motility. Digestive secretions and intestinal absorption have received little investigation in raptors. Gastric secretions have been found to be more acidic (Duke et al. 1975) and to contain more pepsin (Herpol 1964, 1967; Duke et al. 1975) than gastric secretions of granivorous and omnivorous birds; and the pH of the gastric juice of hawks was found to be lower than that of owls (i.e., 1.7 versus 2.4, respectively) (Duke et al. 1975). In an extreme case, this strongly acidic environment enables the Bearded Vulture (*Gypaetus barbatus*) to feed mainly on bones — the only vertebrate known to be able to digest this unpromising diet (Houston and Copsey 1994).

GI motility (i.e., contractile activity) has received considerable attention (Duke et al. 1976b,c; Rhoades and Duke 1977). In more recent years, captive American Kestrels have been used to learn more about this subject (Duke et al. 1997).

Several methods may be used to study GI motility in raptors: (1) tiny strain-gauge transducers (SGT) surgically sutured to the outside surface of the GI tract (called the serosal surface) to monitor smooth muscle contractile activity (Duke et al. 1976b,c), (2) silver bipolar electrodes also sewn onto the serosa to detect electrical potential changes associated with depolarization (contraction) of smooth muscle (Duke et al. 1976c), and (3) radiography using image intensification (a modern type of fluoroscope) and viewing GI contractions on a video monitor or recording observations on video tape (Duke et al. 1976c, Rhoades and Duke 1977). Bioinformation detected by these devices can be recorded on a physiological recorder.

Swallowed foods collect in the crop of hawks and are slowly passed into the stomach. In owls, swallowed food items immediately fill the stomach and lower



Figure 1. GI tracts of (A) domestic turkey, (B) Great Horned Owl, (C) Red-tailed Hawk. Included are (1) pre-crop esophagus, (2) crop, (3) post-crop esophagus, (4) glandular stomach, (5) isthmus, (6) thin craniodorsal muscle, (6a) muscular stomach of raptor, (7) thick cranioventral muscle, (8) thick caudodorsal muscle, (9) thin caudoventral muscle, (10) proximal duodenum, (11) pancreas, (12) distal duodenum, (13) liver, (14) gall bladder, (15) ileum, (16) Meckel's diverticulum, (17) ileocecocolic junction, (18) cecum, (19) colon, (20) bursa of Fabricus, (21) cloaca, (22) vent, greater curvature. From Duke (1978).

esophagus, and after 20 to 30 minutes the entire meal has been moved into the muscular stomach (Rhoades and Duke 1977). In Great Horned Owls, the motilities of the stomach and duodenum are coordinated and the gastroduodenal contraction sequence involves a contraction wave (called peristalsis) that moves first through the stomach, then on into the duodenum (Kostuch and Duke 1975). The peristaltic contraction is more apparent in the muscular stomach as a flattening or indentation moving around the greater curvature (Kostuch and Duke 1975, Rhoades and Duke 1977).

Pellet formation and egestion. The formation and egestion of pellets is a unique gastrointestinal phenomenon in birds, and is particularly well developed in raptors and especially owls (Rea 1973). Analysis of food remains in pellets is a major aspect of many raptor studies (Mikkola 1983, Yalden 2003). Pellets are formed in the stomach from the indigestible bones, hair or feathers of prey (Reed and Reed 1928, Grimm and Whitehouse 1963, Kostuch and Duke 1975, Rhoades and Duke 1977). The prey remains in owl pellets reflect exactly the prey species eaten (Mikkola 1983). But pellet size varies considerably, and curiously has no correlation with the amount of food eaten (Erkinaro 1973). Raczynski and Ruprecht (1974) showed that some prey bones are digested, some skeletal parts more than others, and that food intake estimates based on pellet remains will underestimate the number of prey items swallowed (see also Chapter 8). Duke et al. (1996) also found considerable variability in parts of food items eaten, pellet size, and pellet egestion frequency in captive American Kestrels. Egestion involves both gastric activity and esophageal antiperistalsis (Duke et al.

1976c), and is considerably different from the mechanisms of vomiting in mammals with a simple stomach, or regurgitation of cud in ruminants (Duke et al. 1976c).

Monitoring of gastric motility in owls shows that food intake, or even the sight of food in hungry owls (Duke et al. 1976b), immediately causes a two- to threefold increase in gastric contractile activity. The first mechanical-digestion phase, with relatively rapid and vigorous motility, moves the entire meal into the muscular stomach, crushes or "macerates" it, and thoroughly mixes it with digestive secretions. The second, or chemical-digestion phase, has low amplitude and low frequency contractions that continue to mix gently ingesta with digestive secretions; most digestion is completed during this phase. During the third phase, fluid is evacuated from the stomach, and pellet formation and egestion occur (Fuller and Duke 1978). The length of these phases and the overall meal-to-pellet interval (MPI) varies directly with the amount eaten by an owl, and thus may be used to estimate meal size.

In order to learn more about other factors that regulate pellet egestion and thus alter the lengths of the three phases and influencing MPI, owls were jessed and attached to perches suspended over a sloping chute within a $1 \times 1 \times 2$ -m chamber. Pellets rolled down chutes into wire collecting baskets; a pellet landing in a basket depressed a micro-switch directly under the basket, thereby completing a circuit and activating a marker on a recorder located in another room. The exact time of the event was thus recorded.

Using this technique, six species of owls (Table 1) were fed as many laboratory mice as they wanted during a 30-minute period at two hours after dawn (0900)

| Species | Number of Birds | Mean MPI ± SE (hour) | Number of Pellets |
|---|-----------------|----------------------|-------------------|
| Eastern Screech Owl (Megascops asio) | 2 | 11.86 ± 0.22 | 29 |
| Great Horned Owl (Bubo virginianus) | 4 | 13.25 ± 0.29 | 36 |
| Snowy Owl (Bubo scandiaca) | 2 | 12.02 ± 0.72 | 35 |
| Barred Owl (Strix varia) | 2 | 9.85 ± 0.44 | 25 |
| Short-eared Owl (Asio flammeus) | 1 | 10.22 ± 0.12 | 132 |
| Northern Saw-whet Owl (Aegolius acadicus) | 1 | 10.04 ± 0.32 | 4 |

Table 1. Mean meal-to-pellet intervals (MPI) in owls.^a

^a Data modified from Duke et al. (1976a)

daily. The length of the MPI was shorter in smallersized owls, but, more significantly, the MPI was directly related to meal size, indicating that the state of ingestion of the meal is important in regulating pellet egestion (Table 2; Duke et al. 1976b).

Experiments involving feeding Great Horned Owls on foods of different composition suggest that the presence of undigested food (proteins or fat) in the stomach seems to inhibit pellet egestion, which will not occur until digestion is complete (Table 3; Duke and Rhoades 1977). There also may be a stimulating effect of undigested material on the gastric mucosa, which contributes to pellet ejection. However, other factors also may be involved. Barred Owls (Strix varia) were found to have lengthened MPIs and smaller pellets when fed at a sub-maintenance level until they had lost 10% of their body weight. Analysis of the pellets disclosed that digestion of the meal was more complete in the hungry owls, indicating that the state of hunger may affect MPI (Duke et al. 1980). The constant sight of food may shorten MPI in Short-eared Owls (Asio flammeus) (Chitty 1938).

MPI in owls also may be influenced by environmental stimuli. When Great Horned Owls were fed as many mice as they wanted during a 30-minute period at either dawn or dusk, it was found that MPIs were directly related to meal size but that MPI's were longer for meals eaten at dusk than at dawn regardless of the size of the meal (Duke and Rhoades 1977). This is true for Short-eared Owls, too (Chitty 1938). Thus, the portion of the daily cycle during which gastric digestion and pellet formation occur may affect the MPI.

Kuechle et al. (1987) performed a field study using all of the basic information described above and adapting the techniques used therein for telemetry. In freeflying Barred Owls, movements were monitored via a tail-mounted transmitter and gastric motility was monitored via telemetry of signals from an implanted SGT to determine (1) time of ingestion, (2) time of egestion, (3) measurement of the lengths of phases in gastric digestion and thus, (4) estimation of the quantity consumed. Being able to distinguish movements associated with hunting and feeding from other types of movements is significant in understanding owl behavior, and an estimate of daily food consumption in a free-flying owl is very useful in understanding owl energetics.

In owls the MPI is directly correlated with the quantity eaten, but in hawks the major stimulus for pellet egestion is dawn, regardless of the quantity eaten (Balgooyen 1971, Duke et al. 1976b; Table 4). In a lighttimed room with dawn set at 0700, the MPIs of hawks were 1 to 2 hours shorter when they were fed at 1100 than when they were fed at 0900. In another study involving Red-tailed Hawks in a room with dawn at 0700, feeding time was shifted from 0800 to 1600, and MPI changed from approximately 2200 to approximate-

Table 2. Mean meal-to-pellet intervals (MPI) as related to food consumption (grams DM/kg) in Great Horned Owls and Eastern Screech-Owls fed at 0900 daily.^a

| Species | Number of Birds | Meal Size | Mean MPI ± SE (hour) | Number of Pellets |
|--------------------------------------|-----------------|-----------|----------------------|-------------------|
| Great Horned Owl (Bubo virginianus) | 4 | 10 | 11.76 ± 0.46 | 4 |
| | | 11 – 15 | 12.49 ± 0.35 | 11 |
| | | 16 - 20 | 13.35 ± 0.51 | 12 |
| | | 21 – 25 | 14.71 ± 0.52 | 9 |
| Eastern Screech Owl (Megascops asio) | 2 | 30 - 40 | 10.92 ± 0.25 | 9 |
| | | 41 - 50 | 11.88 ± 0.28 | 13 |
| | | 51 - 60 | 12.92 ± 0.41 | 6 |
| | | 61 - 70 | 13.75 | 1 |

^a Data modified from Duke et al. (1976a)

Table 3. Mean meal-to-pellet intervals for four Great Horned Owls fed (at 1500) two mice, two mouse skins, or two skins stuffed with various diets.^a

| Diet | Mean Mass of Meal (g) | Mean MPI ± SE (hour) | Number of Pellets |
|---|-----------------------|----------------------|-------------------|
| Two 25 g mice | 50 | 15.52 ± 0.45 | 45 |
| Two mouse skins (with skull) | 15 | 15.26 ± 0.20 | 8 |
| Two mouse skins plus two pellets ^b | 25 | 8.19 ± 0.26 | 11 |
| Two pellets only ^c | 10 | 2.75 ± 0.29 | 5 |
| Two mouse skins plus 35 g of horse meat | 50 | 24.34 ± 1.02 | 10 |
| Two mouse skins plus 9 g of suet ^b | 24 | 33.74 ± 2.28 | 11 |

^a Table modified from Duke and Rhoades (1977).

^b Pellets, horse meat, and suet were sewn into the mouse skins with silk suture.

° Pellets were force-fed.

Table 4. Mean meal to pellet intervals (MPI) in hawks with dawn (lights on in the holding room) at 0700.^a

| | | MPI (hour) | | | |
|--|-----------------|---------------------------|----|---------------------------|----|
| Species | Number of Birds | Fed at 0900 Mean MPI ± SE | N | Fed at 1100 Mean MPI ± SE | N |
| Bald Eagle (Haliaeetus leucocephalus) | 3 | 21.7 ± 0.4 | 10 | 20.9 ± 0.38 | 10 |
| Northern Goshawk (Accipiter gentilis) | 4 | 21.6 ± 0.83 | 9 | 20.6 ± 0.17 | 65 |
| Broad-winged Hawk (Buteo platypterus) | 2 | 21.7 ± 0.14 | 13 | 20.8 ± 0.13 | 5 |
| Red-tailed Hawk (B. jamaicensis) | 6 | 22.5 ± 0.09 | 72 | 20.4 ± 0.14 | 59 |
| Roughleg (B. lagopus) | 3 | 21.7 ± 0.08 | 79 | - | - |
| Northern Crested Caracara (Caracara cheriway) | 1 | - | - | 19.6 ± 0.08 | 14 |
| American Kestrel ^b (Falco sparverius) | 1 | 23.6 ± 0.06 | 10 | - | - |

^a Data from Duke et al. (1976a).

^b Dawn was approximately 0800.

ly 1800, respectively, a delay of only 4 hours, suggesting that the birds were "attempting" to egest as early in the day as possible (Fuller et al. 1978). It is theorized that whereas owls may hunt either at night or during the daytime, hawks require daylight for hunting (Fuller et al. 1978). Thus, hawks would benefit by egesting a pellet (i.e., emptying the stomach) early in the day, leaving the rest of the day for capturing and ingesting new prey. Hawks conditioned to eating late in the afternoon respond by shifting egestion time to just prior to the anticipated feeding time (Fuller et al. 1978).

Durham (1983) showed that in Red-tailed Hawks pellet egestion occurred at dawn each day even if the hawks had not eaten the day before or if they had eaten only meat without feathers, fur or bone. Thus, in hawks, egestion motility is not just the end result of having ingested, but is apparently an expression of a circadian rhythm. There are other differences between hawks and owls. Owls normally egest a pellet for each meal, while hawks may eat one to three meals before egesting a pellet (Duke et al. 1975, 1976b). The bones of prey receive little digestion in the stomachs of adult owls, whereas bones are virtually entirely digested in the falconiform stomach (Errington 1930, Sumner 1933, Glading et al. 1943, Clark 1972, Duke et al. 1975, 1976b). This is due to the lower pH in the stomach of hawks (Cummings et al. 1976). Nestling owls also digest bones.

The mechanism of pellet egestion in Red-tailed Hawks follows gastric and esophageal contractile activity very similar to that of Great Horned Owls (Durham 1983), with three clear phases of ingestion motility, chemical digestion and pellet formation, and egestion motility. It is likely that a telemetry study, as performed with Barred Owls, using Red-tailed Hawks or other hawks could provide very useful management information.

Ion and water balances. Little is known about ion and water balances in raptors, but the topic is relevant to management of captive birds. For birds weighing 60 g or more, which includes virtually all raptors, evaporative water loss from the respiratory surfaces and the skin in unstressed individuals can be offset by water produced via oxidative metabolism (Bartholomew and Cade 1963). The moisture in freshly killed prey thus can be used to meet (or partially meet) water loss associated with thermal stress, exercise, or both. Most raptors can be maintained in captivity, and even mate and lay eggs, in the absence of drinking water (Bartholomew and Cade 1957, 1963). Captive Great Horned Owls require 4.4–5.3% of their body weight per day as water (Duke et al. 1973). This intake is lower than that of all but one of 21 species tested by Bartholomew and Cade (1963), including roadrunners (*Geococcyx* spp.), a species adapted to life in an arid environment. Evaporative water loss amounted to approximately 45% of the water ingested with prey in Great Horned Owls (Duke et al. 1973).

Like many other birds, raptors are able to regulate salt and water losses via both the kidney-cloaca system and the nasal salt glands. Urine volumes in Red-tailed Hawks fed beef hearts averaged 30.2 ml/day with sodium and potassium concentrations of 38 and 61 mM/l, respectively. The nasal gland secretions of these birds contained 272 mM/l of sodium and 8 mM/l of potassium (Johnson 1969). Other studies of Red-tailed Hawks have indicated higher sodium and potassium concentrations in both urine (206 and 76 mM/l, respectively) and nasal secretions (380 and 20 mM/l, respectively); similar data were found for eight other falconiform species (Cade and Greenwald 1966). Although functional nasal salt glands are apparently present in all Falconiformes, they have not been reported in Strigiformes.

Nutrition and Food Metabolizability

Nutritional requirements. Small mammals and birds form the bulk of the diet in most raptors. The natural diets (qualitative requirements) of most birds of prey have been studied extensively; some examples are provided in Table 5. The biomass eaten is most important in understanding the energetics of the predator and its impact on the environment. Thus, not only the species of prey and the frequency it occurs in the diet, but also the weight of that prey item must be known. An extensive compilation of prey weights for 35 mammalian and 81 avian prey items was prepared by Steenhof (1983). This includes mean values, determined from a large number of samples in many cases, and separate means for adults (male versus female frequently) and juveniles.

Amounts that must be consumed to maintain a constant body weight under both field and laboratory conditions (quantitative requirements) are known for a few species (Table 5). Food consumption of an individual varies according to level of activity and ambient temperature. Activity is influenced by factors such as day length, prey availability, breeding and nesting, and disturbance. In general, consumption varies inversely with ambient temperature within species and with body size among species (Table 6), as well as directly with activity.

Unfortunately, little is known regarding daily or seasonal requirements for specific nutrients for raptors.

Table 5. Natural foods of some common North American raptors.^a

| | | Percent of Diet | | | | |
|--------------------------------------|-------------------|-----------------|----------------|-------|---------|-------|
| Species | Ref. ^b | Small Rodents | Larger Mammals | Birds | Insects | Other |
| Northern Harrier (Circus cyaneus) | 1 | 98.4 | 0.3 | 1.0 | - | 0.3 |
| Red-shouldered Hawk (Buteo lineatus) | 1 | 97.0 | - | 3.0 | - | - |
| Red-tailed Hawk (B. jamaicensis) | 1 | 95.5 | 1.4 | 3.1 | - | - |
| Roughleg (B. lagopus) | 1 | 98.1 | - | 1.9 | - | - |
| American Kestrel (Falco sparverius) | 1 | 90.3 | - | 9.9 | - | - |
| Barn Owl (Tyto alba) | 2 | 81.6 | 16.4 | 2.0 | - | - |
| Eastern Screech Owl (Megascops asio) | 1 | 3.4 | - | 6.3 | 0.3 | - |
| Great Horned Owl (Bubo virginianus) | 1 | 92.3 | 3.7 | 3.5 | - | 0.7 |
| Burrowing Owl (Athene cunicularia) | 2 | 12.1 | 0.7 | 1.3 | 85.9 | - |
| Barred Owl (Strix varia) | 3 | 53.2 | 7.8 | 24.2 | 4.8 | 10.0 |
| Long-eared Owl (Asio otus) | 1 | 100.0 | - | - | - | - |
| Short-eared Owl (A. flammeus) | 1 | 99.3 | - | 0.7 | - | - |

^a Foods were determined by pellet analysis. Foods such as meat from a carcass and insect parts are thoroughly digested in falconiform stomachs and do not appear in pellets.

^b References: 1 = Craighead and Craighead (1956), 2 = Marti (1969), 3 = Errington (1932).

However, the caloric and nutrient value of some wild and domestic rodents and birds are known (Bird and Ho 1976, Bird et al. 1982; Table 7). These data are useful in assessing the relative nutritive and energy value of wild prey.

The nutrient composition of vertebrate tissues is relatively constant, and as a food source their nutrient balance closely matches that required by birds (Klasing 1998), thus it is unlikely that any macro- or micro-nutrients are limiting in the diet for most species, although a few nutritional disorders have been described in raptors (Cooper 1978). The major difference between prey species is in the relative proportion of fat present, which varies not only between prey species, but also among individuals and between seasons within species. For example, some small passerines can store up to 50% of their body mass as fat prior to migration, making them energetically, high-quality prey.

Almost all raptors eat meat, which is relatively eas-

ily digested, and it might be assumed that all species would show similar digestive efficiencies. This, however, seems not to be the case (Barton and Houston 1994b). Digestive efficiency varies from about 75% to 82%, and this is correlated with the length of the digestive tract. Species with short guts tend to digest their food less efficiently than species with long guts, and consequently need to capture proportionately more prey each day. This may be associated with hunting strategy, for the species with short guts and poor digestive efficiency tend to be species which take a high proportion of birds in flight and need the ability to accelerate rapidly (Barton and Houston 1994a). For such species it may be advantageous to have a lightweight, low-volume gut, even if it results in poor digestive efficiency, because by being more agile they can capture more prey. It does, however, have the consequence that shortgut species are forced to feed on prey items with a high energy content (high body fat), and are unable to main**Table 6.** Food consumption at several ambient temperatures for some adult North American raptors kept outside for one year in Ogden, Utah U.S.A.

| | | | | Amount Eaten per Day | | |
|---|------|--------------------|---------------|----------------------|----------------------|--------------------------|
| Species | Ref. | Diet | Body Mass (g) | Grams | Percent of Body Mass | Ambient Temperature (°C) |
| Bald Eagle (Haliaeetus leucocephalus) | 2 | mice | 3870 | 219.8 | 5.6 | 27 |
| Bald Eagle | 5 | mixed ^c | 3922 | 344.8 | 8.8 | -10 |
| Bald Eagle | 5 | mixed ^c | 3922 | 294.5 | 7.5 | 5 |
| Bald Eagle | 5 | mixed ^c | 3922 | 265.2 | 6.8 | 20 |
| Northern Goshawk (Accipiter gentilis) | 2 | mice | 1100 | 80.2 | 7.3 | 27 |
| Broad-winged Hawk (Buteo platypterus) | 2 | mice | 470 | 29.4 | 6.3 | 27 |
| Red-tailed Hawk (B. jamaicensis) | 2 | mice | 1320 | 75.5 | 5.5 | 27 |
| Roughleg (B. lagopus) | 2 | mice | 1020 | 48.0 | 4.7 | 27 |
| American Kestrel (Falco sparverius) | 2 | chick | 105 | 14.6 | 13.9 | 27 |
| Common Kestrel (F. tinnunculus) | 6 | mice | 204 | 24.3 | 11.9 | 14 |
| Peregrine Falcon (F. peregrinus) | 1 | mice | 680 | 60.6 | 8.9 | 27 |
| Gyrfalcon (F. rusticolus) | 1 | mice | 880 | 70.3 | 8 | 27 |
| Barn Owl (<i>Tyto alba</i>) | 3 | mice | 603 | 60.5 | 10 | _b |
| Barn Owl | 6 | chick | 262 | 28.3 | 10.8 | 14 |
| Eastern Screech Owl (Megascops asio) | 4 | mixed | 153 | 39.0 | 25.4 | 6 |
| Eastern Screech Owl | 2 | mice | 149 | 17.1 | 11.5 | 27 |
| Great Horned Owl (Bubo virginianus) | 2 | mice | 1770 | 71.2 | 4.0 | 27 |
| Great Horned Owl | 3 | mice | 1336 | 62.6 | 4.7 | _b |
| Snowy Owl (B. scandiaca) | 1 | mice | 1900 | 93.1 | 4.9 | 27 |
| Burrowing Owl (Athene cunicularia) | 3 | mice | 166 | 26.4 | 15.9 | _b |
| Barred Owl (Strix varia) | 2 | mice | 741 | 42.9 | 5.8 | 27 |
| Barred Owl | 4 | mixed | 625 | 67.0 | 11.8 | 4 |
| Great Gray Owl (S. nebulosa) | 4 | mixed | 1045 | 77.0 | 7.4 | -10 |
| Long-eared Owl (Asio otus) | 3 | mice | 291 | 37.5 | 12.9 | _b |
| Short-eared Owl (A. flammeus) | 2 | mice | 432 | 50.0 | 11.6 | 27 |
| Northern Saw-whet Owl (Aegolius acadicus) | 2 | mice | 96 | 12.9 | 13.4 | 27 |

^aReferences: 1= Duke et al. (1975), 2 = Duke et al. (1976a), 3 = Marti (1973), 4 = Craighead and Craighead (1956), 5 = Stalmaster and Gessaman (1982), and 6 = Kirkwood (1979).

^b Data are mean values for birds kept outside for one year in Ogden, Utah.

^cChum salmon (Oncorhynchus keta), black-tailed jackrabbit (Lepus californicus), and Mallard (Anas platyrynchos).

Table 7. Partial analysis of nutrient levels in wild and domestic rodents, birds, and an insect.

| | Ratª | Mouse ^a | Chickenª | Day-old Chick ^a | Sparrow ^b | Vole ^b | Grasshopper ^b |
|----------------------------------|---------------|--------------------|---------------|----------------------------|----------------------|-------------------|--------------------------|
| Number of animals | 10 | 30 | 10 | 30 | 11 | 13 | 89 |
| Average mass (g) | 325.7 | 26.7 | 386.7 | 41.2 | 27 | 32 | 0.21 |
| Dry matter % (freeze dried) | 34.4 | 35.4 | 33.5 | 27.6 | 31.6 | 35.7 | 31.9 |
| Crude fat (% DM) | 22.1 | 24.9 | 26.9 | 24.2 | 15.9 | 6.01 | 6.03 |
| Crude protein (N x 6.25% DM) | 62.8 | 56.1 | 56.7 | 62.2 | 64.9 | 57.3 | 75.7 |
| Ash (% DM) | 10.0 | 10.4 | 9.5 | 7.4 | 10.6 | 10.1 | 4.8 |
| Crude fiber (% DM) | 2.4 | 1.7 | 2.0 | 0.8 | 0.43 | 3.85 | - |
| Gross energy (kcal/g DM) | 5.78 | 5.84 | 5.93 | 6.02 | 5.39 | 4.15 | 5.02 |
| Calcium (%) DM wet mass | 2.06 0.69 | 2.38 0.84 | 1.94 0.65 | 1.36 0.38 | 2.94 0.94 | 2.85 1.02 | 0.31 0.098 |
| Phosphorus (%) DM wet mass | 1.48 0.51 | 1.72 0.61 | 1.40 0.47 | 1.00 0.28 | 2.35 0.74 | 2.66 0.95 | 1.27 0.41 |
| Ca:P ratio | 1.39 | 1.38 | 1.39 | 1.36 | 1.3 | 1.1 | 0.2 |
| Zinc (mg/kg) DM wet mass | 129.2 13.3 | 134.6 47.7 | 158.0 52.8 | 106.9 29.9 | 109.8 34.7 | 105.5 37.7 | 200.2 63.9 |
| Copper (mg/kg) DM wet mass | 4.5 1.5 | 8.0 2.8 | 4.5 1.5 | 3.2 0.9 | 12.6 3.98 | 13.7 4.89 | 50.3 16.1 |
| Manganese (mg/kg) DM wet mass | 7.5 2.5 | 11.7 4.1 | 9.0 3.0 | 3.0 0.8 | 11.4 3.6 | 14.9 5.32 | 25.1 8.01 |
| Iron (mg/kg) DM wet mass | 175.7 58.9 | 239.1 84.6 | 146.8 49.1 | 121.8 34.0 | 592.0 187.2 | 332.3 118.7 | 331.4 105.8 |
| Thiamine (mg/kg) DM | 13.3 | - | 8.5 | 16.0 | - | - | - |

^a From Bird and Ho (1976) ^b From Bird et al. (1982); House Sparrow (*Passer domesticus*), meadow vole (*Microtus pennsylvanicus*), red-legged grasshopper (*Melanoplus femurrubrum*)

tain their body weight if fed on prey with low fat levels (Taylor et al. 1991). This may explain why many falcons specialize on small passerines and are rarely found feeding on carrion or low-energy prey.

The ceca of owls apparently make little contribution to food digestion since metabolizability of a mouse diet was not significantly different between cecectomized and intact Great Horned Owls (Duke et al. 1981). Water balance also was unaffected by cecectomy.

Kirkwood (1981) calculated maintenance metabolizable energy (ME) based on food intake for several diets at several ambient temperatures for nine strigiform and 22 falconiform species using the linear regression equations ME = $110 \text{ W}^{0.679}$, where ME is expressed in kcal/day and W (weight) in kg. Data for Falconiformes and Strigiformes were pooled as separate regressions and were not significantly different. Wijnandts (1984) made similar calculations for 13 strigiforms and 26 falconiforms under caged conditions eating either mice or rats. Metabolizable energy also was calculated from published data on food consumption using a caloric value of 8.4 kJ/g for mice or rats and assumed metabolizability of 76%. Linear regression equations derived for falconiforms and strigiforms were ME = $9.722 \text{ W}^{0.577}$ (r = 0.918) and ME = 8.63 W^{0.578} (r = 0.958), respectively, where ME is in kJ/bird/day and W is in g.

SUMMARY

We still have much to learn about the gastrointestinal physiology of raptorial birds. Prey availability (both population size and vulnerability), the nutritive value of the prey, and its metabolizability by raptors all must be considered in evaluating raptor energetics. In these birds with such uniquely carnivorous food habits, further research in this field should prove most fruitful. However, with the tragic passing of co-author Gary Duke, who led the world in the field of avian gastrointestinal physiology in 2006, and no one on the immediate horizon appearing to follow in his footsteps, it may be some time before significant advances in this field are again achieved.

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