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GASTROINTESTINAL MORPHOLOGY AND MOTILITY IN AMERICAN KESTRELS RECEIVING HIGH OR LOW FAT DIETS[1]

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Abstract. Fifteen yearling, male American Kestrels (*Falco sparverius*) were fed either intact day-old chicks (*Gallus domesticus*) (high-fat diet) or chicks with the yolk removed plus a piece of lean turkey meat approximately equivalent in volume to the yolk (low-fat diet). This was done for 33–37 days to determine the influence of dietary fat on the gastrointestinal gross anatomy and contractile activity of the kestrels. Fat content of the diet appeared to have little effect on either anatomy or contractions. Observations of contractile activity, via Image Intensification Radiology, revealed a unique reflux of duodenal contents associated with every duodenal flux in every gastroduodenal contraction cycle (approximately 3–4 min^{-1}). This presumably improved mixing of ingesta with digestive secretions and hastened digestion of ingested nutrients which would be advantageous to a small bird with a high mass-specific metabolic rate. The duodenum was enlarged relative to the size of this organ in other raptors, possibly to accommodate to this process. The colon also was relatively larger in this species, perhaps to permit final processing of the diet and water absorption from the greater quantity of digesta passed from the small intestine.

Key words: Falco sparverius, *duodenal reflux, image intentification radiology, duodenum, colon.*

INTRODUCTION

Avian species possess a variety of adaptations for digestive processing of their diets, including microbial fermentation of cellulose in the hindgut (Clench and Mathias, 1995), very slow gastric emptying of high fat diets (Leach's Storm-Petrel chicks *Oceanodroma leucorhoa,* Duke et al. 1989) which presumably improves intestinal digestion of dietary fat, or more rapid passage of seeds than of fruit pulp through the small intestine (Cedar Waxwings *Bombycilla cedrorum,* Levey and Duke 1992), thus foregoing efforts to digest the seeds and focusing instead on digesting the pulp. Oral egestion of pellets by raptors and other carnivorous birds also appears to be a digestive adaptation allowing birds to avoid having to process hair and bones and pass them through the entire GI tract.

The small intestinal reflux, a type of intestinal motility first described in domestic turkeys *Meleagris gallapavo* (Duke et al. 1972), also appears to be a mechanism for improving intestinal digestion of nutrients. It has been described in a few other species, including Leachs' Storm-Petrels (Duke et al. 1989) and Ostriches *Struthio camelus* (Duke et al. 1995), but not in raptors.

The mechanism and regulation of pellet egestion and gastric motility are well understood in raptors (Grimm and Whitehouse 1963, Balgooyen 1971, Duke et al. 1976a, 1976b, 1976c, Duke and Rhoades 1977, Fuller and Duke 1978, Fuller et al. 1978, Duke et al. 1980). Rectal antiperistalsis (peristalic contractions directed towards the mouth rather than towards the anus), which appears to occur in all birds (except pos-

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sibly ostriches, Duke et al. 1995), also has been described in both strigiforms and falconiforms (Duke 1989), but little is known about intestinal contractile activity in raptors.

Intestinal refluxes (a rapid movement of intestinal contents towards the mouth) occur about three times per hour in fed domestic turkeys and appear to occur more frequently in birds eating a high-fat diet (Duke et al. 1989). Such refluxes can be induced in domestic turkeys by intraduodenal injection of solutions of lipid, amino acids, and hypertonic saline, or by balloon inflation in the intestinal lumen (Duke and Evanson 1972, Duke et al. 1973). Fat is presumably ingested regularly by raptors and is likely to be quite important in meeting their energy needs.

The objectives of this study were to describe intestinal morphology and motility of kestrels and to determine whether morphology and motility are influenced by fat content of the diet. Kestrels were sacrificed at the completion of experiments to determine if high or low fat diets may have differentially affected gross GI tract morphology (Clench and Mathias 1995).

MATERIALS AND METHODS

Fifteen yearling, male American Kestrels *Falco sparverius* (hereafter called kestrels) obtained from a captive colony at the Avian Science and Conservation Centre of McGill University were selected for this study because of their ready availability, homogenous parentage for approximately 20 years (D. Bird, pers. comm.), and because their small size was ideal for our radiographic technique of monitoring gastrointestinal (GI) motility. The birds were maintained on a diet of laboratory mice for five weeks (15 September–20 October) while they acclimated to our individual cages (46 × 38 × 46 cm deep), holding room (5.5 × 3.7 × 2.5 m high), a controlled environment (25–27°C, 45–50% relative humidity, photoperiod with lights on from 07:00–20:00), and feeding schedule (daily at 08:00). Cages were cleaned weekly and fresh water for drinking and bathing was provided daily. These conditions were maintained during the experiment (from 20 October until birds were euthanized on 2, 5, or 6 December 1994), but a single one-day-old White Leghorn chick was fed intact (high-fat diet) or with the yolk removed (low-fat diet) to each kestrel each day. A piece of lean turkey breast meat approximately equivalent in volume to the removed yolk also was fed daily to the low fat-fed group. The high-fat diet contained approximately 26 times more fat then the low-fat diet.

Gastrointestinal motility (i.e., contractile activity) and the movements of gut contents were studied by Image Intensification Radiology (IIR) (Philips, Super M-100, Shelton, CT). Images were displayed on a video monitor and recorded on standard VCR video tape. Our use of this shared equipment was limited to 07:30–09:00 each day; observations were conducted on 16 days. During observations, conscious subjects sat on a wooden perch in a cardboard box 30 × 40 × 30 cm wide. Four of the 15 kestrels (two high-fat fed and two low-fat fed) were observed in both the fed and fasted conditions. Fasted birds did not receive the usual 08:00 feeding, but were fed after observations were completed (about 09:15). Immediately before observations were to begin, approximately 1.0 ml of $BaSO_4$ (1 $BaSO_4$/2 H_2O) solution was administered orally into the crop via a polyethylene catheter (12 cm long, 2 mm o.d., 1.4 mm i.d.) attached to a 3-ml syringe.

We observed and recorded time required for the crop to empty all administered $BaSO_4$ solution, filling times for the gizzard, duodenum, ileum and colon, and emptying times for these organs when possible (i.e., if these times occurred before our allotted time to use the IIR equipment had expired). We also observed and recorded gastric and duodenal contraction frequencies and durations, and the nature of the contractions (e.g., peristalic, antiperistalic, coordination with other parts of the tract). Recordings were further analyzed to confirm emptying times and to more carefully analyze sequences such as the gastroduodenal contraction sequence. The contraction frequencies and durations were compared among three 15-min observation periods, viz., "early, middle and late", corresponding to just after filling of an organ, when it was partially empty and when it was nearly empty, respectively.

Mean gastric contraction frequencies (number of contractions per minute) and durations (time required for a contraction to occur, not including relaxation time between contractions) and duodenal flux/reflux frequencies and durations were compared via split-plot analysis of variance using the General Linear Models procedure (SAS Institute, Inc., 1994). The model for the split-plot design was diet as the whole plot, bird within diet for error A, feeding status for the split-plot, interaction of diet by feeding status, and the residual for error B. Statistical comparisons were considered significantly different when $P < 0.05$. The significance of differences between mean lengths and weights of each region of the GI tract was determined using a Bonferroni correction applied to Student's t-test ($P < 0.05$). Values listed are means ± SD, except where noted.

The birds were weighed upon arrival in our laboratory, two weeks later, monthly thereafter and at the time of sacrifice. Five birds were sacrificed (CO_2 inhalation) on each of three successive days (2, 5 and 6 December 1994) between 07:30–10:00. The birds were not fed on the day of sacrifice and any food remaining in their cage was removed just before the lights came on in their room to ensure that they were in the fasted condition. Weights and lengths of intestinal segments, proventriculus, gizzard and cloaca, as well as weights of pancreas and liver were determined. Abdominal fat deposits were removed and weighed.

RESULTS

The crop, proventriculus and gizzard of the kestrels were similar in appearance and relative size to those of other falconiforms (Duke 1986b). The duodenum, however, was relatively quite long accounting for about one-half of the total length of the intestine and was visibly larger in diameter than the ileum (Fig. 1). Rather than consisting of a single intestinal loop as in other falconiforms and most other birds as far as we know, it consisted of a loop within a loop (Fig. 1) and both loops surrounded the pancreas. The latter empties exocrine secretions into the distal duodenum via three ducts; two bile ducts empty at this point as well. This anatomical arrangement is like that in other birds (Duke 1986a).

At the junction between the ileum and the colon was what appeared to be a single cecum. Histological examination of this structure confirmed that it was a cecum. It contained an extremely thin smooth muscle layer, nodules of lymphoid tissue such as is characteristic of ceca in other avian species (Duke 1986a), and an epithelial lining with sparse, palmate villi. Further evidence that this structure was a cecum was provided by histological examination of intestines immediately proximal and distal to it. Proximally, the intestine had numerous long thin villi and well developed smooth muscle layers characteristic of the ileum. The intestine distal to the cecum had short, lobular, less numerous villi and a thin smooth muscle layer characteristic of the colon. While the cecum was relatively small, its lumen always had contents. The colon, like the duodenum, was quite long compared to other falconiformes and other avian species, except Ostriches. At the junction between the colon and the cloaca, a small, dense structure, presumably the bursa of Fabricius, was found as in every species.

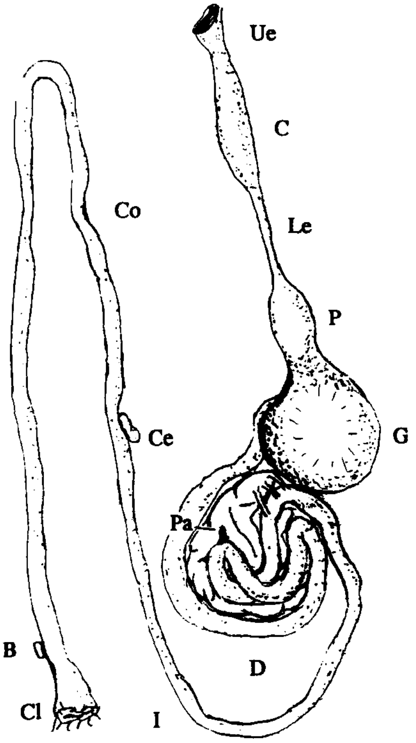

FIGURE 1. Line drawing of the gastrointestinal tract of a kestrel. Ue = upper esophagus; Le = lower esophagus; C = crop; P = proventriculus; G = gizzard; D = duodenum; Pa = pancreas; I = ileum; Ce = cecum; Co = colon; Cl = cloaca; B = bursa of Fabricius.

On average, kestrels in the high-fat fed group ate the yolk 95.7 ± 0.1% of the time. Frequently the yolk sac was torn and yolk covered most of the chick carcass. Kestrels in the low-fat fed group ate the piece of lean turkey meat only 30.6 ± 0.3% of the time on average. The mean mass of the piece of turkey breast meat

TABLE 1. Mean lengths and weights (±SD) of each region of the gastrointestinal tract of American Kestrels (*Falco sparverius*) fed high-fat and low-fat diets for 50–54 days. High-fat diets consisted of whole day-old chicks. Low-fat diets consisted of chicks with yolk sac removed plus 15 g turkey breast meat.

Measurement*	High-fat	*n*	Low-fat	*n*
Length (cm)				
Proventriculus	1.5 ± 0.2	7	1.5 ± 0.3	8
Gizzard	2.0 ± 0.3	7	2.2 ± 0.2	8
Duodenum	12.0 ± 1.1	7	12.0 ± 1.6	8
Ileum	11.8 ± 2.1	7	12.6 ± 2.0	8
Colon	15.8 ± 1.8	7	16.2 ± 0.9	8
Cecum	0.5 ± 0.1	5	0.5 ± 0.2	8
Cloaca	1.7 ± 0.5	6	1.6 ± 0.4	8
Mass (g)				
Liver	2.57 ± 0.45	7	2.49 ± 0.26	8
Pancreas	0.36 ± 0.07	7	0.34 ± 0.09	8
Proventriculus	0.50 ± 0.07	7	0.52 ± 0.04	8
Gizzard	1.39 ± 0.12	7	1.54 ± 0.11	8
Duodenum	0.92 ± 0.14	7	0.95 ± 0.20	8
Ileum + jejunum	0.48 ± 0.13	7	0.54 ± 0.13	8
Colon	0.60 ± 0.18	7	0.59 ± 0.11	8
Cecum	0.02 ± 0.01	6	0.02 ± 0.01	6
Cloaca	0.18 ± 0.04	6	0.16 ± 0.03	7
Body fat	0.74 ± 0.44	7	0.41 ± 0.40	8
Body mass (at sacrifice)	108.34 ± 6.40	7	107.21 ± 7.40	8

* Comparisons were made between diets (i.e., columns) and considered significantly different when ($P < 0.05$). No significant differences were found.

was 10.30 ± 2.65 g, whereas the yolk weights at 21 days of incubation were less, averaging 2.57 ± 1.53 g. The yolks, however, contained relatively much more fat than the lean meat. Yolks contain 50% neutral fats and 21% phospholipid (Romanoff 1960). This amounts to an average of 1.82 g of fat per yolk. Lean turkey breast meat contains about 1.66% fat (Ag. Handbook 1994), or only 0.07 g of fat in the pieces of meat that were fed to the kestrels in this study. So, even when the lean meat was eaten, the kestrels in the low-fat fed group consumed much less fat than those in the high-fat fed group; the high-fat fed birds received at least 25 times (1.82 g vs. 0.07 g) more fat than the low-fat fed birds when both groups ate all of the food presented to them each day. Exclusive of the very small amount of fat in the chick carcass, which was equal in the high-fat vs. low-fat diet, fat amounted to 4.76% vs. 0.20% of the diet in the high-fat fed vs. the low-fat fed birds. Despite the greater fat intake by kestrels on the high-fat diet, no discernible differences in the gross anatomy of the GI tract or in GI motility were observed. Although high-fat fed birds had almost twice as much fat in the body cavity at sacrifice as low-fat fed birds, this difference was not statistically significant (Table 1). Total fat in the body cavity was less than 1% of body mass for all birds (Table 1).

The frequency of gastric contractions was about four per minute in the "early" period following $BaSO_4$ administration regardless of fed or fasted condition or high-fat vs. low-fat diet. This frequency slowed somewhat by the late period, but the change was not statistically significant (Table 2). Correlated with this, gastric contraction cycle duration lengthened during the "late" period and this change was statistically significant in high-fat fed, fasted subjects ($P = 0.047$) (Table 2).

After $BaSO_4$ administration, we were able to observe that portions of the crop contents emptied into the post-crop esophagus, then into the proventriculus at the end of the contraction of the gizzard. The proventriculus, gizzard and duodenum contracted in a coordinated sequence as in other raptors (Kostuch and Duke 1975, Durham 1983). This gastroduodenal contraction sequence began with a contraction wave spreading through the proventriculus. Then a wave of contraction moved around the greater curvature of the gizzard to the duodenum (Fig. 2). Presumably a wave was moving across the lesser curvature as well, but because of the small size of this area, we could not observe it. As the

TABLE 2. Mean (±SE) gastric and duodenal contraction frequencies and durations for American Kestrels (*Falco sparverius*) fed low- or high-fat diets and either fed or fasted at the time of the experiments.

Measurements	High-fat fasted	*n*	High-fat fed	*n*	Low-fat fasted	*n*	Low-fat fed	*n*
Gastric cycle durations* (sec)								
Early	16.09 ± 3.24	8	18.07 ± 1.69	21	16.96 ± 2.25	13	17.55 ± 1.59	21
Middle	19.45 ± 1.70	14	18.02 ± 1.09	28	17.67 ± 2.58	6	21.91 ± 1.49	7
Late†	25.09 ± 0.79	14	20.03 ± 0.69	29	20.83 ± 1.09	7	22.11 ± 0.57	19
Gastric contraction frequencies (#/min)								
Early	4.53 ± 1.02	9	3.94 ± 0.53	23	4.20 ± 0.71	15	4.05 ± 0.50	24
Middle	3.61 ± 0.37	16	3.81 ± 0.24	27	4.13 ± 0.56	7	3.25 ± 0.33	8
Late	2.79 ± 0.16	16	3.48 ± 0.14	26	3.41 ± 0.22	8	3.23 ± 0.12	22
Duodenal flux durations (sec)††	1.91 ± 0.12	12	1.33 ± 0.11	20	1.16 ± 0.12	13	1.00 ± 0.83	6
Duodenal reflux durations (sec)	4.91 ± 1.62	12	9.02 ± 1.42	20	5.49 ± 1.56	13	6.53 ± 1.10	6
Duodenal flux/reflux frequencies (#/min)	4.19 ± 0.45	12	3.80 ± 0.40	20	3.62 ± 0.44	13	3.34 ± 0.31	6

Comparisons were made between columns (i.e., between diets and fed versus fasted states).

* Duration of each contraction/relaxation cycle.

† Gastric cycle durations in high-fat fasted birds were significantly higher than in high-fat fed birds ($P < 0.05$).

†† Duodenal flux durations were significantly higher in high-fat fasted birds than in either low-fat fed ($P < 0.03$) or low-fat fasted ($P < 0.05$) birds.

wave reached the duodenum, a contraction started at the pylorus and spread rapidly through the upper one-half or two-thirds of the duodenum and sometimes through the whole duodenum and into the upper ileum (Fig. 3A–C). This rapid "sweep" required 1–2 seconds (Table 2). Immediately after this, and for the next 5–9 seconds, one to four contractions moved orad (towards the mouth) through the duodenum in rapid succession refluxing much of the contents back into the proximal duodenum or into the gizzard (Fig. 3A–C). It was evident that not all of the duodenal contents had refluxed because the ileum slowly filled with contents.

Ileal motility was not remarkable. However, both peristalsis and antiperistalsis were observed in the colon. As the colon filled, it enlarged greatly and peristalsis could be seen as a single large wave indenting the colon lumen and moving aborad (away from the mouth) in the distal colon. Antiperistalsis was evident as a series of small waves barely indenting the serosal surface of the colon (Fig. 4). Defecation was observed only one time before our scheduled use of the IIR equipment was completed. During defecation the distal 2–3 cm of the colon contracted to expel the contents of that region. The fecal mass was held in the cloaca for about 1 second before being expelled.

As indicated above, gastric contents fluxed into the duodenum following each gastric contraction, then much of that content refluxed back to the gizzard. The flux was more rapid than the reflux (Table 2). Flux was significantly longer in duration in both high-fat fasted birds than in either the low-fat fasted ($P = 0.049$) or low-fat fed birds ($P = 0.026$). The frequency

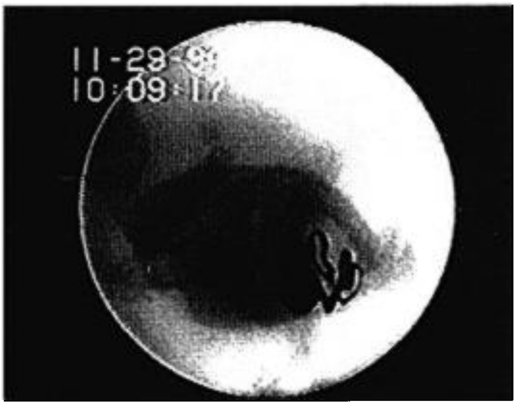

FIGURE 2. Left-lateral radiographic image of the upper GI tract of a kestrel. The crop is empty, but the esophagus is faintly outlined with $BaSO_4$ and the gizzard and proximal duodenum (lower right) are clearly outlined. The left side of the gizzard has a contraction.

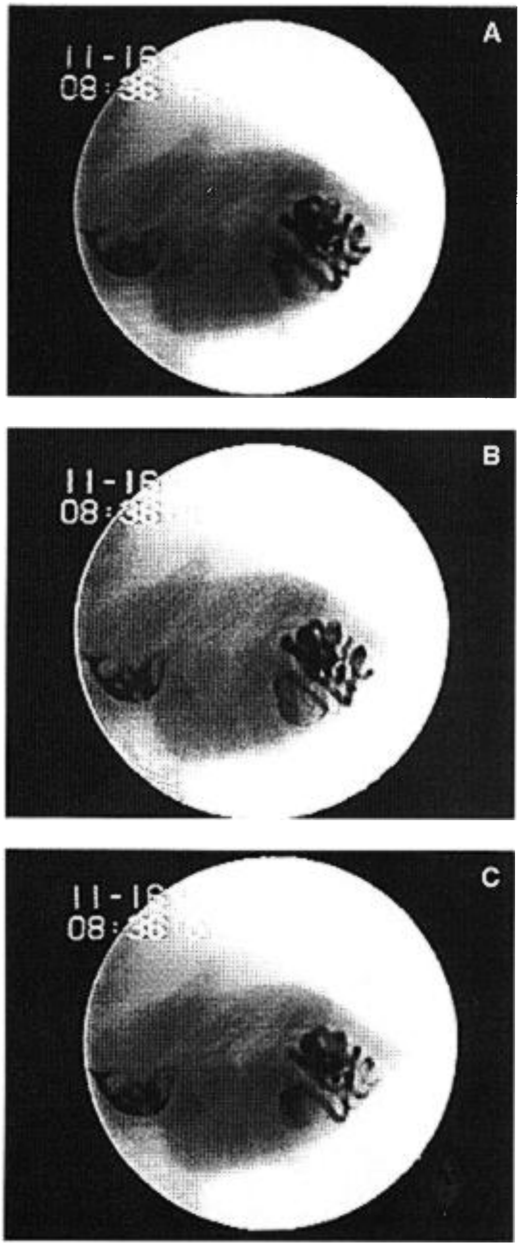

FIGURE 3. Left-lateral radiographic image of the crop (on the left, with an air bubble at its end nearest the head), gizzard (faintly outlined on the center-right), and duodenum (far right). A. Proximal duodenum outlined as flux from gizzard into duodenum is occurring. B. Proximal duodenum relatively empty of $BaSO_4$ as flux from gizzard is ending. Distal loops (far right) are filled with $BaSO_4$. C. Distal loops are now emptying as contents reflux toward the gizzard and the proximal duodenum, attached to the gizzard, is darker as duodenal contents reflux towards the gizzard.

FIGURE 4. Right-lateral radiographic image of the colon of a kestrel showing three small indentations that are antiperistaltic contractions in the terminal colon.

of the flux/reflux cycle ranged from 3.3 to 4.2 per minute (Table 2).

Filling and emptying times of regions of the GI tract with $BaSO_4$ marked contents were difficult to determine precisely. Usually, filling of the stomach and duodenum obscured filling or emptying of other parts of the tract, or made it difficult to positively identify lower duodenum vs. upper ileum. In general there did not appear to be great differences in filling or emptying times between high-fat fed and low-fat fed birds (Table 3).

DISCUSSION

The gross anatomy of the American Kestrel was considerably different from that of other falconiforms in four aspects: (1) the duodenum comprised approximately one-half of the total length of the small intestine and it was coiled in a double loop. In Red-tailed Hawks *Buteo jamiacensis* and Great Horned Owls *Bubo virginianus*, the duodenum comprises about one-fifth of the total length of the small intestine and exists as a single loop (Duke 1986b). (2) The duodenum is slightly larger in diameter than the ileum in these other raptors, but the duodenum is noticeably larger (about 50%) than the ileum in kestrels. (3) The pancreas fills the entire duodenal loop in kestrels, but only about one-fourth of the proximal part of the loop in Red-tailed Hawks. (4) The colon is relatively long in kestrels as compared to the colons of Red-tailed Hawks, Great Horned Owls and domestic fowl (Duke 1986b). An examination of the GI tract

TABLE 3. Mean (±SD) filling and emptying times for $BaSO_4$ solution in GI regions of American Kestrels (*Falco sparverius*).

Measurement	High-fat	*n*	Low-fat	*n*
Filling times (sec)				
Crop	10.00 ± 14.14	2	21.00 ± 1.73	3
Proventriculus	76.00 ± 79.19	2	20.00 *	1
Gizzard	95.67 ± 56.43	3	42.33 ± 24.79	3
Duodenum	84.33 ± 59.47	3	103.75 ± 45.76	4
Ileum	291.00 ± 156.98	2	•	0
Colon	2,161.00 *	1	1,991.00 ± 49.50	2
Emptying times (sec)				
Crop	139.00 ± 29.70	2	146.00 ± 71.84	4
Proventriculus	601.00 *	1	•	0
Gizzard	772.00 *	1	726.00 *	1
Duodenum	617.00 *	1	2,246.00 *	1
Colon	3,010.00 *	1	•	0

* No SD, *n* = 1.
• No data available.

of an immature Peregrine Falcon *Falco peregrinus* after completing the present study disclosed that it also had the loop within a loop structure of the duodenum, but only about one-third of the loop encompassed the pancreas. The colon of this specimen also was relatively long like that of the kestrel and the cecum was 7 mm long and filled with homogeneous, viscous, light brown solution very similar to typical cecal contents of many species (Duke 1989). Single ceca are not unique to Falconidae (Clench and Mathias 1995).

Intestinal refluxes have not been reported to occur in other raptors, however the gastroduodenal contraction cycle has been described for Red-tailed Hawks (Durham 1983) and Great Horned Owls (Kostuch and Duke 1975, Rhoades and Duke 1977), and the flux/reflux contractions associated with every gastric cycle in kestrels would have been evident during observations of motility in these other species if they were present. They were seen almost immediately in the first observation period of the present study.

The purpose of the persistent flux/reflux in kestrels is unknown. Because the main function of the duodenum in all birds is digestion (Duke 1986a), flux/reflux in the kestrel duodenum presumably improves digestibility of the diet by more thoroughly mixing digestive secretions from the proventriculus, pancreas, and duodenum with food in the stomach and duodenum. Because of the smaller size and higher mass-specific metabolic rate of kestrels (Duke 1986b) compared to the larger raptors mentioned above, this adaptation to improve digestion would seem to be appropriate and important. However, further studies are required to fully clarify the function of this motility pattern. It also would be interesting to determine if other small raptors have persistent flux/reflux intestinal motility.

Duodenal refluxing has not been reported to occur in mammals, but has been described in a variety of birds. It is a regularly occurring event in chickens *Gallus domesticus* at 2 to 3 per hour, in turkeys at approximately 3 per hour (Duke 1986a) and in Leach's Storm-Petrels at approximately 8 per hour (Duke et al. 1989). During 26 hours of radiographic observations of GI motility in Cedar Waxwings, only one reflux was observed (Levey and Duke 1992) and similarly only one was observed in Ostriches during 11 hours (Duke et al. 1995). Thus, while duodenal refluxes are not unusual in birds, the nearly continuous fluxing and refluxing seen in kestrels is apparently unique. The greater frequency of refluxing in petrels was believed to be due to their typically very high fat diet, however reflux frequency did not appear to be correlated with dietary fat content in kestrels (Table 2).

The fourth anatomical peculiarity seen in kestrels was the very long colon. It comprised approximately 40% of the total intestinal length in kestrels versus only about 15% of the total intestinal length in Red-tailed Hawks and Great Horned Owls (Duke 1986b). The colon is important in water conservation in birds (Duke

1986a). Because of the higher mass-specific metabolic rate of kestrels and the higher environmental temperatures associated with their preferred habitat in open fields, increased water conservation via a large colon would be important to them. A second possible function of this enlarged colon, and the small cecum, could be breakdown of ingesta resistant to digestion in the upper GI tract such as the chitin of insect exoskeletons by microbial chitinase. Further studies are required to determine all functions of the relatively long colon.

In most birds examined thus far (Duke 1989), defecation involves expulsion of nearly all of the contents of the entire colon. In kestrels with their relatively longer colon than other birds, only the very distal 2–3 cm of colonic contents are expelled. It appears that the colon of kestrels segregates those contents that have been the most thoroughly digested and which have had most of their moisture absorbed into the most distal colon for expulsion while retaining less digested, less dry digesta more proximally in the colon for further processing. Cedar Waxwings have a similar defecation pattern generally expelling 50% or less of their colonic contents per defecation (Levey and Duke 1992).

In conclusion, the unique structure of both the duodenum and the colon of kestrels may have resulted in unique functions as well. It is likely that within the duodenum a very thorough mixing of ingesta with digestive secretions occurs via fluxing and refluxing to both hasten and increase digestibility. Within the elongated colon the needs for water reabsorption are probably easily met and some additional degradation of the more resistant portions of the diet like chitin may also be accomplished. The unique functions of these organs warrant further study.

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