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Gastroduodenal Motility and Glandular Stomach Function in Young Ostriches

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Gastroduodenal motility has been described in several avian species. In domestic turkeys (*Melagridis gallapavo*; Duke et al. 1972, Dziuk and Duke 1972), chickens (*Gallus gallus*; Roche et al. 1971), Cedar Waxwings (*Bombycilla cedorum*; Levey and Duke 1993), and Leach's Storm-Petrels (*Oceanodroma leuchoroa*; Duke et al. 1989), the sequence begins with contraction of the pair of thin muscles of the muscular stomach. Next, a wave of contraction starts through the duodenum and while this wave progresses, the pair of thick muscles contracts. Last, a wave of contraction moves orad to aborad through the glandular stomach (Duke et al. 1972, Dziuk and Duke 1972). Ingesta moves from the muscular stomach into the duodenum during contraction of the thin muscles, from the muscular stomach to the glandular stomach during contraction of the thick muscles, and from the glandular stomach back to the muscular stomach during glandular stomach contraction. Members of the Strigiformes (Duke et al. 1976), Falconiformes (Duke 1989), and Ciconiiformes (Rhoades and Duke 1975) lack the thin and thick muscles in their muscular stomach, however, and their contractile pattern consists of a wave of contraction that starts at the orad end of the glandular stomach and proceeds through the muscular stomach and duodenum. Most avian species possess thin and thick muscles and the muscular stomach is two to three times larger than the glandular stomach (McLelland 1979). However, in some species (e.g. Struthioniformes, Procellariformes, and Sphenisciformes), the glandular stomach is larger than the muscular stomach. A major function of the large glandular stomach in storm-petrels and other procellariforms is to retain their very high fat diet and slowly pass it to the duodenum where fat digestion occurs. This avoids loading too much fat into the duodenum at once which would reduce digestibility (Duke et al. 1989).

The large glandular stomach of Ostriches (*Struthio camelus*) may temporarily store newly ingested food, but postmortem examinations of several birds showed no evidence that it serves as a fermentation chamber (Duke pers. obs.). The paired ceca and colon, however, clearly serve this function (Skadhauge et al. 1984). The gastroduodenal contraction sequence has not been described in Ostriches, and the purpose of the large glandular stomach is unknown. Therefore, our ob-

TABLE 1. Duration of muscular-stomach-contraction cycle and frequency of muscular-stomach contractions ($\bar{x} \pm$ SD) for hydrated ($n = 30$) and dehydrated ($n = 12$) Ostriches.

Bird	Duration of cycle (s)		Contractions/min	
	Hydrated	Dehydrated	Hydrated	Dehydrated
1	28.8 ± 5.50	38.4 ± 5.74	2.08 ± 0.40	1.56 ± 0.23
2	28.8 ± 4.50	22.4 ± 2.69	2.08 ± 0.32	2.68 ± 0.32

jectives were to describe the sequence of gastroduodenal contractions and to determine the function of the large glandular stomach.

Methods—We used two male Ostriches, 7 and 8 weeks old (body mass $\bar{x} = 7$ kg) at the start of this study (30 June 1993) and 11 and 12 weeks old at the end (2 August 1993; body mass $\bar{x} = 10$ kg). They were provided with a commercially prepared concentrated mash diet (Mazuri Ostrich and Ratite Diet, starter #5584, PMI Feeds, St. Louis, Missouri) and water *ad libitum* and maintained in an animal-holding room (Department of Veterinary PathoBiology, University of Minnesota, St. Paul, Minnesota) under controlled environmental conditions. Relative humidity was kept at 45 to 50%, temperature was held at 25 to 27°C, and lights were on from 0600 to 2000 CST daily. Birds were acclimated to these conditions for eight days before we began experiments. They were taken outside for approximately 1 h every other day to receive sunlight and to graze on the lawn.

Gastroduodenal motility was observed in a left-lateral orientation via image intensification radiology (Philips Super M100, Philips Medical Systems, Shelton, Connecticut). Observations were made from 0800 to 1100 on six different days over two weeks on normally hydrated Ostriches. Each bird was observed for approximately 1.5 h each day. The first observation period was used to acclimate the birds to the experimental conditions and to familiarize the observers with radiographic anatomy of the Ostriches. During one experiment, water was withheld from 1300 one day until 0900 (during radiography) the following day. This included a 10-h period of darkness in which they normally would not have consumed food and water (Degen et al. 1989).

Contrast media were used to enhance radiographic images of the contents of the glandular and muscular portions of the stomach or the duodenum. A barium sulfate ($BaSO_4$) powder, which is radio-opaque, was mixed with the mash diet so that movements of food within the gut could be observed. Some of this powder became disassociated from the food and became suspended in the liquid of the lumen so that fluid could also be identified and fluid movements discerned. Also, on one occasion, an aqueous suspension of $BaSO_4$ was administered per os with a syringe and polyethylene tubing (1.2 mm i.d., 1.5 mm o.d., 20 cm long).

Radiographic images were viewed on a video monitor and recorded (Panasonic VCR, AC-6010S, Secaucus, New Jersey) on video tape for subsequent analysis of contraction sequences or patterns and determination of gastric contraction frequencies and durations. Selected images were captured using a digitization program (MacVision Color Digitizer, SCSI Interface version 1.1 and MacVision Image Processing Software version 4.0, Koala Acquisitions, San Jose, California). Images from the video tape were then printed and photographed.

Results and discussion.—The gastroduodenal contraction cycle of Ostriches and fluxes of ingesta between the glandular and muscular portions of the stomach appeared to be similar to these processes in turkeys (Duke et al. 1972, Dziuk and Duke 1972). Gastric contraction frequencies and the duration of the gastroduodenal contraction cycle (Table 1) in our two subjects were also similar to frequencies and durations in normally hydrated turkeys (ca. 3 contractions/min and 24 s in duration in turkeys; Duke et al. 1972). Contraction frequency increased in one Ostrich and decreased in the other following dehydra-

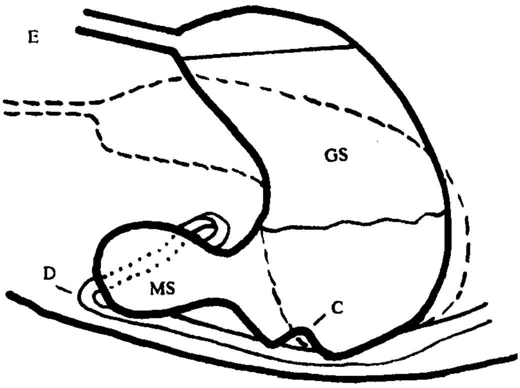

Fig. 1. Line drawing of composite of left-lateral radiographic images showing shape of glandular and muscular portions of stomach. Straight line near dorsal surface of glandular stomach represents fluid level in this organ in hydrated bird, whereas lower irregular line represents level of food. Dashed line represents configuration of glandular stomach when bird sits down. (E) Esophagus; (GS) glandular stomach; (MS) muscular stomach; (C) contraction in glandular stomach; (D) duodenum.

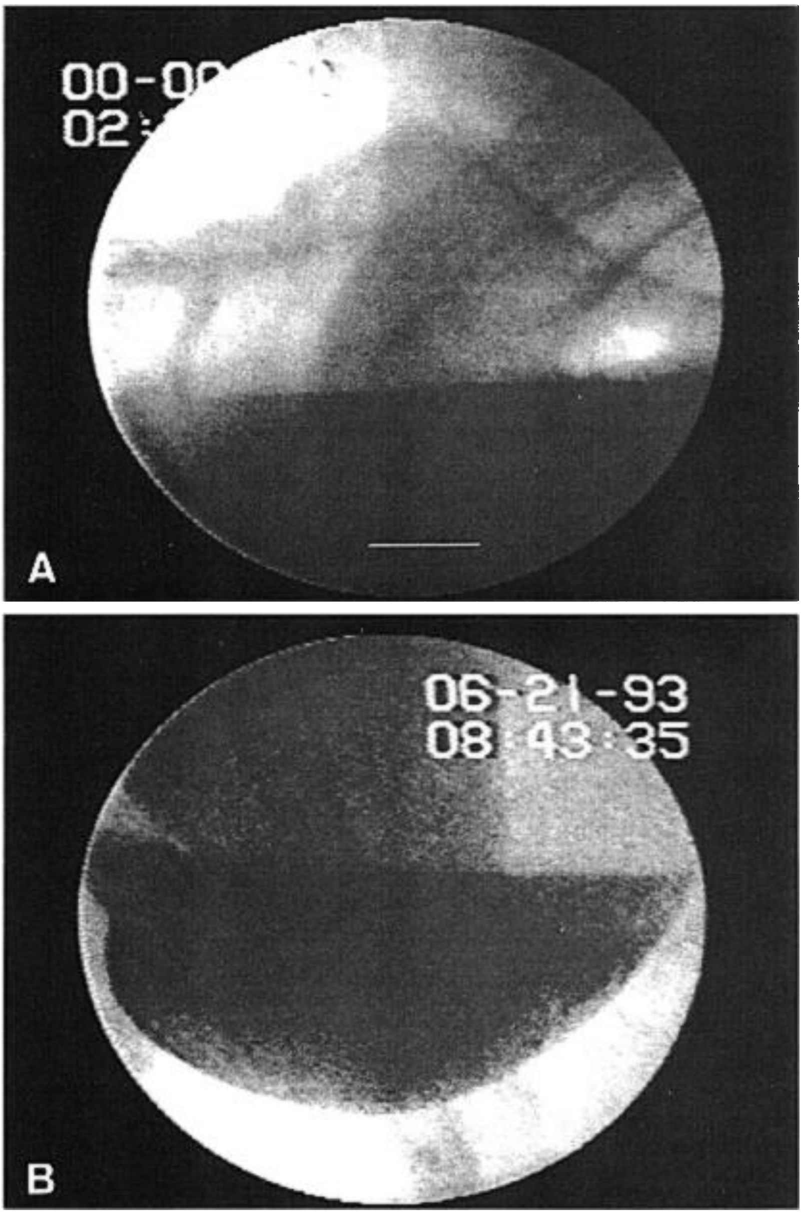

Fig. 2. (A) Left-lateral radiographic image of anteriordorsal area of glandular stomach showing gastroesphageal area and dorsal surface of glandular stomach. Dark area in lower half of image is water within glandular stomach. White scale-bar represents 2 cm. (B) Image of ventral curvature of glandular stomach.

tion (Table 1). No cause for the different responses between the two birds was apparent.

A type of intestinal motility unique to birds, and apparently occurring in many species (e.g. Duke et al. 1972, Rhoades and Duke 1977, Duke et al. 1989), is the duodenal reflux. This involves orad flow of ingesta from the upper half of the small intestine into the stomach and presumably improves overall digestibility of the diet by exposing it two to three times to duodenal and pancreatic digestive enzymes. Only one duodenal reflux was observed during our observation sessions with both Ostriches; there are approximately 3 refluxes/h in turkeys (Duke et al. 1972). Intestinal fluxes however, were somewhat hard to discern due to the density of the intestinal mass in such a large bird, so it is likely that more occurred that we did not observe.

The most striking finding of our study was the large

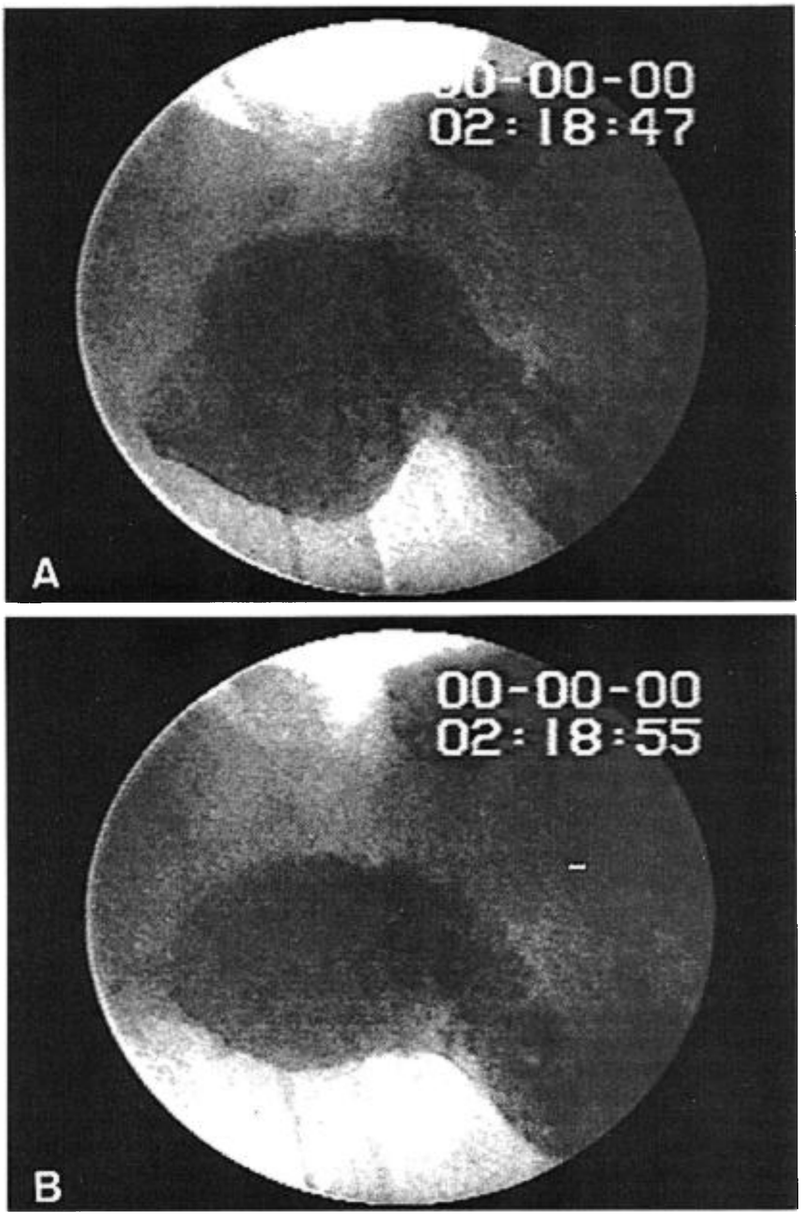

Fig. 3. Left-lateral radiographic image of muscular stomach during contraction of (A) pair of thin muscles and (B) pair of thick muscles.

volume of water always present in the glandular stomach of hydrated Ostriches (Figs. 1 and 2). Apparently, this organ serves as a water reservoir and, since it is so sizable, could serve well in this capacity. When our birds were deprived of water for 20 h, however, no water level was discernible in the glandular stomach. This gives some indication of the duration of water storage in the reservoir. In adults or larger juveniles with a lower metabolic rate and relatively less body surface area, the reservoir may last longer.

The radiographic images of contractions of the thin and thick muscle pairs were consistently recognizable (Fig. 3). However, contraction of the thick muscles, viewed in the left-lateral aspect (Fig. 3B), appeared oval rather than "femur"-shaped as described in turkeys (Dziuk and Duke 1972). The femur shape is seen in a frontal radiographic view in Ostriches.

Ostriches are well adapted to semi-arid and arid conditions, generally inhabiting dry wadi beds and desert savannah plains (Sauer and Sauer 1966a, b, Bertram 1980). These omnivorous birds have a varied diet consisting mainly of shrubs, succulents and seeds and, to a lesser extent, of insects and lizards (Cramp and Simmons 1977). Ostriches drink large volumes of water (Sauer and Sauer 1966a) and generally drink daily (Cloudsley-Thompson and Muhamed 1967). They are usually within 24 km of water (Berry and Louw 1982); however, they can be found 80 km from a water source (Sauer and Sauer 1966a).

Ostriches can withstand substantial dehydration (up to 30% body mass loss) and then have the ability to drink water approximately equalling the body mass lost during dehydration (Cloudsley-Thompson and Muhamed 1967). The rapid ingestion of a large volume of water (17% of body mass) following dehydration only caused a slight decline in plasma osmolality (Withers 1983), suggesting that the water entered the plasma slowly. Our observations in this study revealed that ingested water was stored in the glandular stomach and then released slowly until the next water ingestion. In this way, Ostriches can graze over a large radius from a water source because of their great mobility, and can replenish the glandular stomach in one ingestion. The mass of this reservoir would be of little consequence to a flightless species. So far as we know, no flighted desert birds have adopted this strategy.

This pattern appears to be analogous to the one described for the black Bedouin goat (*Capra hircus*). This small ruminant can graze in the harsh Sinai desert for four days without drinking, which allows a grazing area of approximately two days walk from a water source. Every four days the goats drink a volume of water that replenishes what has been lost. The water is then stored in the rumen, which releases it slowly until the next ingestion (Chosniak and Shkolnik 1978, Shkolnik and Choshniak 1987).

Such a reservoir function for the glandular stomach of the Ostrich has not been described in other avian species. It has been suggested, however, that the glandular stomach may serve to store food in Emus (*Dromaius novaehollandiae*; Herd 1985) and the lower small intestine may act as a region for water storage (Herd and Dawson 1984). Both Ostriches and Emus have a long neck and neither has a true crop, so the usual storage function performed by the crop in other birds may be performed by the glandular stomach in these ratites. This reasoning is strengthened by the fact that only a small proportion of the mucosa of the glandular stomach of ratites has secretory cells (Fowler 1991).

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Hummingbirds Eating Ashes

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The nectar-rich diet of hummingbirds results in their producing large volumes of hypo-osmotic cloacal fluids except under conditions of high heat stress. Their need to excrete or avoid absorbing the excess water is comparable to that of freshwater fish and frogs with urine production reaching 84% of body mass per day (Calder and Hiebert 1983, Beuchat et al. 1990)! Some of the ions lost in excretion are replaced by those present in the nectar. The insect portion of the diet also provides additional salts. Several fortuitous field observations suggest that some hummingbirds may also replace essential ions by consuming wood ashes during the stress of nesting.

On five separate occasions, I or my students have observed nesting female hummingbirds repeatedly licking, and probably consuming, powdery, gray wood ashes. Four of the five birds' nests contained two eggs each. The fifth nest was inaccessible to observation. The field observations were as follows: (1) Broad-tailed Hummingbird (*Selasphorus platycercus*) in Englemann spruce (*Picea engelmanii*) woodland, Shannon Camp, 3 km W of Heliograph Peak, Graham Co., Arizona (elevation 2,800 m), 7 July 1978. (2) Blue-throated Hummingbird (*Lampornis clemenciae*) in oak woodland, South Fork Camp, 8 km S of Portal, Cochise Co., Arizona (elevation 1,700 m), 11 July 1978. (3) Costa's Hummingbird (*Calypte costae*) in Low Colorado Desert wash, Milpitas Wash, near Highway S 78, 40 km SW of Blythe, Riverside Co., California (elevation 100 m), 26 March 1980. (4) Anna's Hummingbird (*C. anna*) in suburban garden, Claremont, Los Angeles Co., California (elevation 460 m), 8 Dec 1982. (5) Anna's Hummingbird in white alder (*Alnus rhombifolia*) woodland, Day Canyon, Etiwanda, San Bernardino Co., California (elevation 880 m), 27 April 1983.

In each case the bird made repeated visits to a dead campfire or barbecue pit and licked the fine ash that had fallen from the charred wood. The birds' behavior appeared purposeful in that all of them left the nest, flew 25 to 60 m directly to the ashes, licked for a few seconds, and returned to the nest. The routine was repeated several times per hour through the middle of the day, and was observed for up to 10 days. Feeding forays were interspersed with these trips to the ash heaps. When on the nest, the birds seemed to make no notable adjustments of nest material nor did they appear to deposit anything onto the nest material, so I am confident that material from the ash heaps was not being used in nest construction. None of these birds were using bird feeding stations during the periods of observation. I have never seen a male or a nonnesting female engaged in this behavior.

Wood ash is surprisingly rich in calcium. For example, CaO often comprises one-half to three-quarters of the total ash. Crystalline calcium carbonate and calcium oxalate frequently occur in wood (Wise 1944:436) and, thus, contribute significantly to ash composition. Sodium is also variably present in ash,