PELLET FORMATION IN A GREAT HORNED OWL: A ROENTGENOGRAPHIC STUDY

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In the literature on owls, there has been much interest in the formation in the upper gastro-intestinal tract of pellets which contain indigestible material and which are subsequently regurgitated. This feature of gastro-intestinal function has interested bird physiologists, and analysis of the pellets has been used to monitor feeding habits (Errington *et al.*, 1940). Although pellet formation is not limited to the order Strigiformes, most information concerning this aspect of avian physiology comes from work on owls. Studies have centered on such problems as factors affecting the meal-pellet interval (Chitty, 1938), pellet analysis, physico-chemical properties of digestive juices, and anatomical distinctions between pellet forming and non-pellet forming birds (Guerin, 1928).

It is possible from indirect evidence to make a reasonable estimate of the sequence of events involved in the 10 hour process of the formation of a pellet from the indigestible portion of an animal. A review of the available literature, however, fails to reveal an accurate account of events *in vivo* as seen by radiographic methods. The opportunity for such a study was afforded when a full-grown Great Horned Owl (*Bubo virginianus*) was received for study.

Methods

The owl, which appeared to be in splendid condition, was securely tethered to a wooden platform by means of leather jesses. Following a period of two days with this restriction, the bird was blindfolded, carried to an animal radiology laboratory in The University of Michigan Medical Center, and left to become accustomed to its surroundings in semi-darkness. During this period of acclimatization, the X-ray tube, casette, and casette holder mounted on a ring stand were moved about the bird to simulate experimental procedure. This experience was repeated twice, each time with the owl spending four to six hours in the laboratory. On the second occasion, a rodent was offered, and was promptly killed by the owl, but not eaten. After four days of food deprivation, the owl was returned to the laboratory for experimentation.

X-rays were made in a lateral projection with the film casette pressed against the wing surface (this did not disturb the owl) on the side opposite to the X-ray tube. The X-ray tube was placed approximately 60 cm (two feet) from the owl. Exposures were made at 50 KV with 100 milliamperes for 0.1 second.

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Also a recently shot Great Horned Owl was received for autopsy. Figure 1A is an X-ray of this bird in the lateral position with a tube in the esophagus. The tip of the tube lies in the region of the proventriculus. An introduced radio-contrast material (Hypaque) outlined the size and contour of the lumen of the ventriculus (as shown by arrows). This procedure established the position of the gastro-intestinal tract in relation to other anatomical landmarks. An autopsy was performed; the findings will be considered briefly later.

OBSERVATIONS

Figure 1B is an X-ray of the bird prior to feeding. Residual food (the area of density in the lower part of the ventriculus) is not unusual in owls forced to go for long periods without food (Chitty, 1938). The owl was fed seven laboratory mice, which were consumed within seven minutes. Figure 1C, taken one hour after feeding, shows an expanded ventriculus. Small bones can be seen (as a dense reticular pattern) scattered within the ventriculus. Figures 1D and 1E, taken two and three hours after feeding, show a reduction in the volume of the ventriculus, and give some suggestion of condensation of the small bones. In Figure 1F, taken five hours post-prandial, arrows delineate the outline of the forming pellet. Figure 1G, taken eight hours after feeding, demonstrates continued condensation of materials, the pellet size and configuration being essentially fixed by 10 hours (Figure 1H). Films taken up to 16 hours (when the pellet was expelled) fail to show a significant change in its size. The pellet remained in the superior area of the ventriculus (approximately its position in Figure 1H) until regurgitation. The recovered pellet measured 4.5 cm in length and 2.5 cm in diameter; Figure 1I is an X-ray of the pellet. Regurgitation of the pellet was not observed.

The second experiment, performed after a period of food deprivation, was carried out by injecting two mice intraperitoneally with 2.5 ml of radio-contrast material. The mice were promptly taken by the owl. Spillage of this material into the small intestine seemed a simple way of determining how quickly disruption and digestion occur. Figure 2B shows radio-contrast material in the ventriculus of the owl, five minutes after the mice were swallowed. It is apparent from the irregular pattern of distribution, that contrast material has remained in the abdominal cavity of the mice. By 10 minutes (Figure 2C) however, not only has contrast material diffused evenly throughout the ventriculus, but it also appears in the proximal portion of the small intestine (arrows).

GENERAL CONSIDERATIONS

The observation that the owl carried the pellet approximately six hours after it appeared to be completed, and the presence of indigestible material

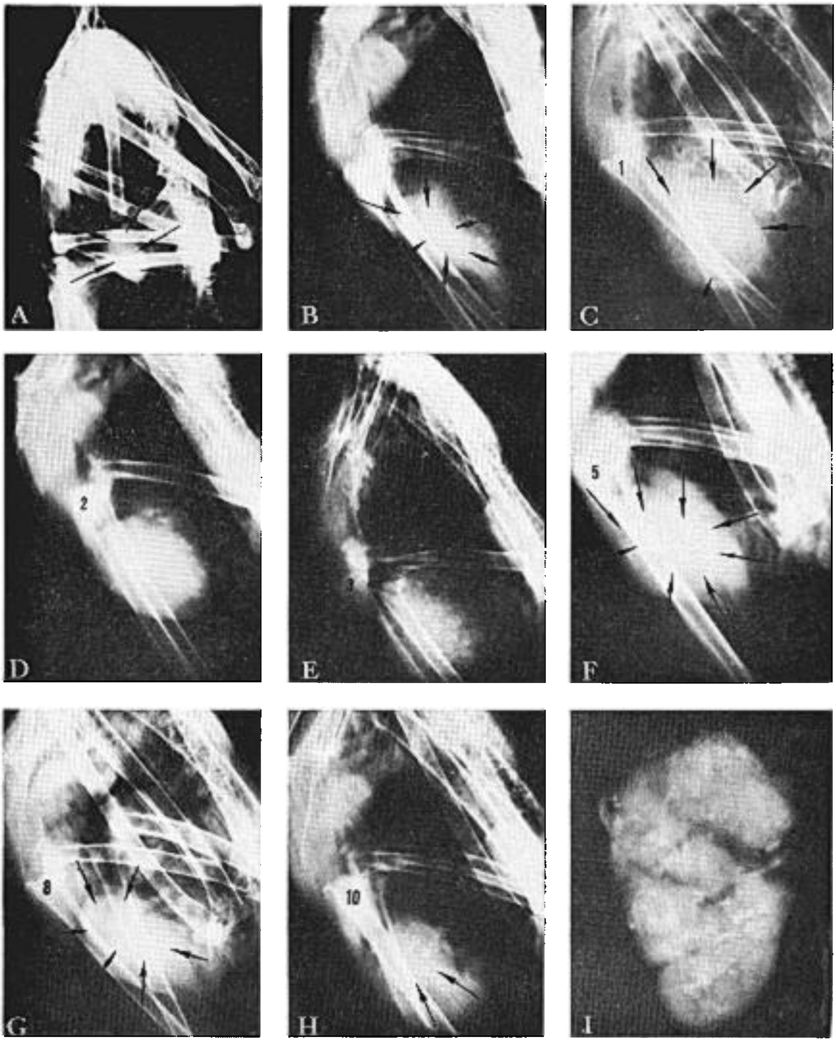

Figure 1. X-rays of Great Horned Owls. A. Autopsy specimen, intubated, showing contour of ventriculus filled with radio-contrast material. B–I show *in vivo* studies (all times refer to hours after feeding). B. Hungry owl before feeding. X-ray suggests the presence of residual food material in the ventriculus. C. Appearance of the ventriculus one hour after swallowing seven mice. D. Two hours. E. Three hours. F. Five hours. Arrows delineate forming pellet. G. Eight hours. Further condensation of pellet material is seen. H. Ten hours. Pellet is essentially complete (no further reduction in size was seen in later films). I. Pellet, recovered sixteen hours after feeding.

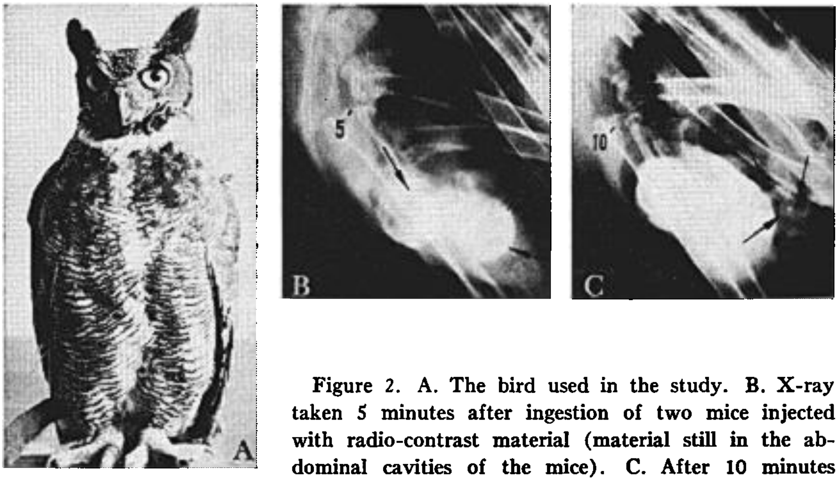

Figure 2. A. The bird used in the study. B. X-ray taken 5 minutes after ingestion of two mice injected with radio-contrast material (material still in the abdominal cavities of the mice). C. After 10 minutes (contrast material fills the proximal portion of the owl's small intestine).

within the ventriculus between feedings, tend to support Chitty's observations (1938) that the meal-pellet intervals increase during periods of food shortage.

Autopsy, confined mainly to the gastro-intestinal tract, confirmed Reed and Reed's observations (1928) that in the Great Horned Owl the pyloric outlet is very small (1.5 mm) and arises from the superior surface of the ventriculus. As Reed and Reed pointed out, this anatomical arrangement appears to be an effective barrier against the passage of bulky food particles.

The gross and microscopic anatomy of the proventriculus and ventriculus proved interesting. The ventricular wall, composed of an inner circular and outer longitudinal muscle layer, was 2 to 4 mm in thickness, and there was no evidence of hypertrophy in the areas of the sphincters between the proventriculus and ventriculus, or the ventriculus and duodenum. The ventriculus was securely bound to the abdominal wall by dense fibrous connective tissue. The spacious, thin-walled esophagus and the superior portion of the proventriculus were lightly anchored to the thoracic cage by thin sheets of connective tissue. Proventricular glandular pits were prominent, and the cellular elements of these exocrine units were eosinophilic, suggesting a serous secretory character. Basophilic, mucus-producing cells lined the fine villus-like structures of the ventriculus.

It is perhaps worthy of note that there is no apparent anatomical modification of the gastro-intestinal tract significantly related to pellet formation (see Guerin, 1928). Somewhat similar pellets are formed by a variety of predatory birds that consume parts or all of vertebrate animals, for example by hawks, owls, gulls, cormorants, crows and ravens, and probably others. Gallinaceous birds, which do not form pellets, have stomachs grossly similar to the short, thick-walled stomach of crows. The presence, on the other hand, of a relatively thin-walled ventriculus in the Great Horned Owl (as in most hawks and owls; Farner, 1960: 428), lined with villus-like structures, supports the view that this organ functions in these, as in other birds, primarily in mixing.

One curious aspect of digestion in Great Horned Owls is that during pellet formation in adult birds the stomach pH approximates neutrality or is slightly alkaline (Guerin, 1928; Wilson and Niosi, 1961). In young birds (three months of age), F. H. Wilson (pers. comm., 1962) noted that stomach pH during feeding, sampled by means of a gastric tube, was acidic (pH 4). In older birds, the pH became neutral, a condition, as he noted, that excludes pepsin as the active proteolytic enzyme. Wilson and Niosi (1961) concluded that the essentially neutral character of the ventriculus during active digestion is due to reflux into the ventriculus of alkaline secretions of the small intestine and pancreas.

In summarizing, the process of pellet formation in owls seems to occur as follows: an owl retains its animal meal within the ventriculus by closure of the sphincter between the ventriculus and proventriculus; the pyloric opening, which is small and arises superiorly, probably remains open during most of the digestive process. In this actively contracting and relaxing pouch collect enzymatic secretions arising from the glands of the proventriculus, small intestine, and pancreas. Although the general enzymatic action in digestion is little known, there is evidence that in young owls the gastric pH is distinctly acidic, becoming more neutral in older birds.

As digestion proceeds, the nutrient effluent is pumped into the small intestine by ventricular contractions. Indigestible solids, e.g., bone, fur, teeth, nails, and chitinous materials, collect in the inferior portion of the ventriculus, and are gradually forced into a tight pellet form. The length of time between feeding and regurgitation of a pellet is subject to both internal and external factors (Chitty, 1938). In the hungry Great Horned Owl in our laboratory, pellet formation was essentially complete eight hours after feeding.

Before regurgitation, an event Guerin (1928) held to be voluntary, the pellet lies in the superior portion of the ventriculus immediately below the sphincter. At expulsion, the sphincter is relaxed, and ventricular contraction, with accessory contractions of the abdominal wall and proventriculus, force the pellet upward in a series of steps until it is finally discharged; the process in the Great Horned Owl takes approximately four minutes.

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LITERATURE CITED

CHITTY, D. 1938. Pellet formation in Short-eared Owls, *Asio flammeus.* Proc. Zool. Soc. London, **108** (Series A): 267–287.

ERRINGTON, P. L., F. HAMERSTROM, and F. N. HAMERSTROM, JR. 1940. The Great Horned Owl and its prey in north-central United States. Agric. Expt. Sta., Iowa State College Agric. and Mech. Arts, Bull. no. 277. Pp. 759–850.

FARNER, D. S. 1960. Digestion and the digestive system. *In* The biology and comparative physiology of birds. Vol. I. A. J. Marshall (ed.). New York, Academic Press.

GUERIN, G. 1928. La vie des chauttes. Regime et croissance de l'effreys commune. Paris, P. Lechevalier.

REED, C. I., and B. P. REED. 1928. Mechanism of pellet formation in the Great Horned Owl *Bubo virginianus.* Science, **68:** 359–360.

WILSON, F. H., and P. N. NIOSI. 1961. Some observations on gastric digestion in the horned owl. Amer. Zool., **1:** 399 (abstract).

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