FACTORS INFLUENCING PELLET EGESTION AND GASTRIC pH IN THE BARN OWL

CHARLES R. SMITH AND MILO E. RICHMOND

THE volume of literature considering the food habits of owls approaches prodigious proportions (see Earhart and Johnson, 1970). Much of this information has been derived from analysis of the pellets of non-digestible matter which these raptors egest periodically. A number of authors have reviewed this technique and its applications (Craighead and Craighead, 1956; Errington, 1930, 1932; Fisher, 1893, 1896; Glading, Tillotson and Selleck, 1943; Moon, 1940). In spite of the widespread interest in raptor-pellet analysis and application of this procedure for estimating food intake of these birds in the wild, very little information is available on the factors relative to the processes of pellet formation and egestion in birds of prey (Farner, 1960).

The Great Horned Owl (*Bubo virginianus*) is the only owl for which pellet formation has been studied (Reed and Reed, 1928). Other papers considering pellet "formation" in owls have been concerned largely with the intervals between feeding and pellet egestion and have not dealt directly with the digestive processes involved in pellet formation or the factors which determine pellet egestion (Chitty, 1938; Howard, 1958; Sensenig, 1945). Two extensive life history studies of the Barn Owl (*Tyto alba*) by Guérin (1928) and Wallace (1948) offer some information relative to pellet formation and egestion in that species. It is the intent of this paper to present further information relative to the processes involved in pellet formation and egestion in the Barn Owl.

MATERIALS AND METHODS

The Barn Owl used in this investigation was obtained near Johnson City, Tennessee, at the age of approximately 20 days, as determined by plumage description (Bent, 1938; Roberts, 1955). The bird was kept in captivity and fed small mammals and birds (both alive and dead), beef liver, and a commercial liquid vitamin supplement ("ABDEC") until it was about 8 weeks old. At the age of 8 weeks, the bird was moved from its outdoor cage into a laboratory at East Tennessee State University and tests which required regular handling were begun. The owl adapted readily to laboratory conditions and required no special housing or handling technique. A laboratory colony of prairie voles (*Microtus ochrogaster*) provided the primary food source for the owl. At first, the voles were fed to the owl dead; later, the owl learned to take and kill live voles which were either released into the cage or placed on the floor of the lab.

To determine the pH of the gastric contents, a stomach sample was obtained by inserting a 10-mm pipette equipped with suction bulb into the esophagus of the bird until it reached the region of the gizzard. By this method samples of volume from 0.5 to 1 ml could be withdrawn from the region of the gizzard and from the proventriculus. The bird showed no adverse effects from this procedure which was sometimes conducted

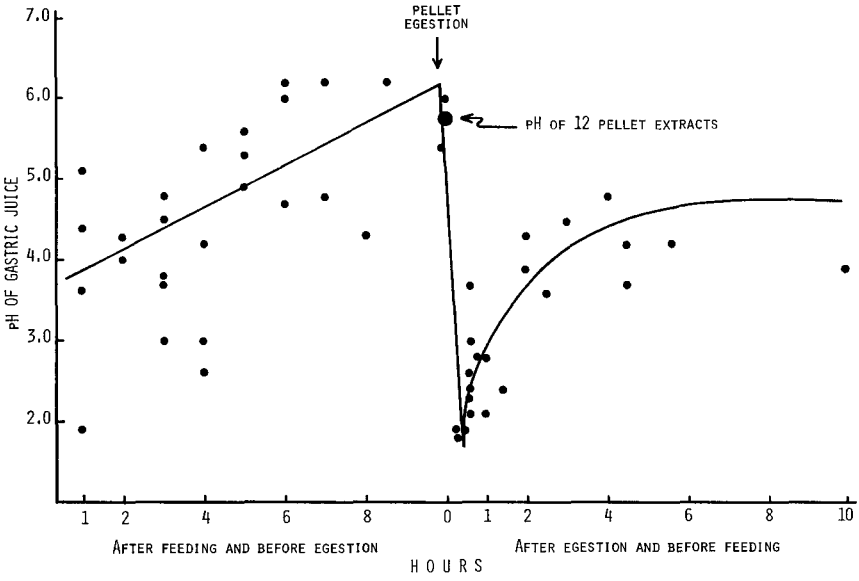

FIG. 1. Changes in gastric pH of the Barn Owl before and after feeding (curve fitted by inspection).

at hourly intervals for a 12-hour period. The pH of the samples was determined by using a Corning "Model Six" portable pH meter. The presence or absence of free HCl in stomach samples was detected with standard Topfer's solution, but the sample size was insufficient for accurate titration of the quantity of free HCl. The pH of extracts squeezed manually from newly egested pellets was also determined with the pH meter.

RESULTS AND DISCUSSION

Gastric acidity.—A total of 58 stomach samples, taken both before and after the bird had eaten, provided data for the cumulative graph of gastric acidity in Figure 1. The data show that the pH gradually rises after feeding and continues to increase until pellet egestion. Within an hour after pellet egestion, there is a precipitous drop, followed by another rise until the pH values stabilize in the vicinity of 4.0. Farner (1960), reported a gastric pH range of 3.53–4.90 for the Barn Owl. Our data (Fig. 1) show a much wider range of pH extending from 1.9 to 6.2. The low pH values immediately following egestion indicate a gastric state especially conducive to high peptic activity and proteolysis since the optimum state for these activities is in the vicinity of pH 2.0 (Farner, 1960).

Figure 2 shows the results of two separate days of pH recordings at hourly intervals under different conditions. Equal amounts of food were given at

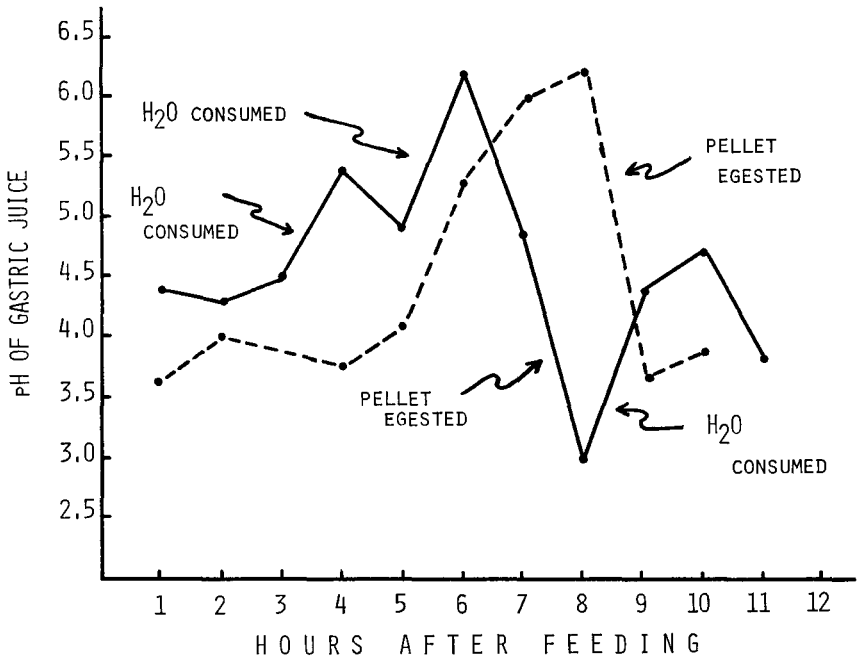

FIG. 2. Hourly changes in the pH of the gastric juice of the Barn Owl with (solid line) and without (dashed line) water available.

the same time on each day; however, in one case drinking water was available and in the other it was not. Excess food was not available in either case. With water available, the increase in pH during hours 4 and 6 and the generally higher pH values prior to pellet egestion followed known water consumption. Clearly, the water consumed reduced the acidity of gastric contents. The graph of gastric acidity obtained in the absence of water closely resembles the graph of Figure 1, which also was made in the absence of drinking water. The pH values of extracts from freshly egested pellets were very similar to the pH values of stomach samples taken within an hour before pellet egestion. Contrary to the observations of Reed and Reed (1928) on the Great Horned Owl, free HCl was found in stomach samples from the Barn Owl on six separate occasions when pH values ranged from 1.9 to 3.4. Free HCl was present most often immediately after pellet egestion or soon after the owl had been shown a live vole.

Classically, there are three phases to the secretion of gastric juice: the cephalic, the gastric, and the intestinal (Houssay, 1955). The cephalic phase involves the stimulus of gastric secretion as a result of external factors, such as the sight or smell of food, mediated through the cerebral cortex. The

mechanisms involved form the basis for classical Pavlovian conditioning. According to Farner (1960), a true cephalic phase of gastric secretion is lacking in the domestic fowl. Walter (1939), however, reported gastric juice secretion in ducks in the response to auditory stimuli. Our results would indicate that a cephalic phase of gastric secretion is present in the Barn Owl. We learned, for example, that the pH of gastric contents decreased markedly within one-half hour after we entered the room in which the owl was kept. This decreased pH, indicative of increased HCl secretion in anticipation of food, was observed numerous times when live voles were placed in view of the owl but outside its cage. Free HCl was also present in stomach samples taken after the owl had been shown a live vole, and the same marked drop in gastric pH was observed in the bird after it had been fasted and then was allowed to observe live prey.

Pellet formation.—There is some disagreement in the literature as to where in the digestive tract pellet formation occurs. Welty (1963) suggests that the pellet is formed in the gizzard. Wallace (1955) states that pellet formation occurs in the proventriculus. Guérin (1928) felt that the gizzard played a significant role in pellet formation because of its highly muscular qualities. He also reported that dissection revealed pellet material in both the proventriculus and gizzard at different times, but he did not relate its place of occurrence to either times of feeding or pellet egestion.

Probing with the pipette while taking gastric samples indicated the presence of pellet material in both the proventriculus and the gizzard at different times. However, probing immediately before egestion indicated that the pellet was located in the proventriculus and not in the gizzard.

Reed and Reed (1928) reported that the "stomach" musculature in the Great Horned Owl is weak and not capable of exerting a great deal of force. These authors apparently were referring to the glandular stomach (proventriculus) since the gizzard is noted for its muscular structure. The muscular ability of the proventriculus of the Barn Owl closely resembles that of the Great Horned Owl. This seems to argue against the proventriculus playing any major role in the process of pellet formation. However, it is possible that the proventriculus could function as a repository for a freshly formed pellet prior to egestion. It is our contention, then, that the pellet is formed by the muscular action of the gizzard during digestion. At some stage after the completion of digestion, the freshly formed pellet passes out of the gizzard into the proventriculus where it remains until the proper stimulus for egestion is received.

Pellet egestion.—Initial observations suggested that the time of feeding had some influence on the time of subsequent egestion. To test this possibility, food was offered at various times of the day and night. All feedings between

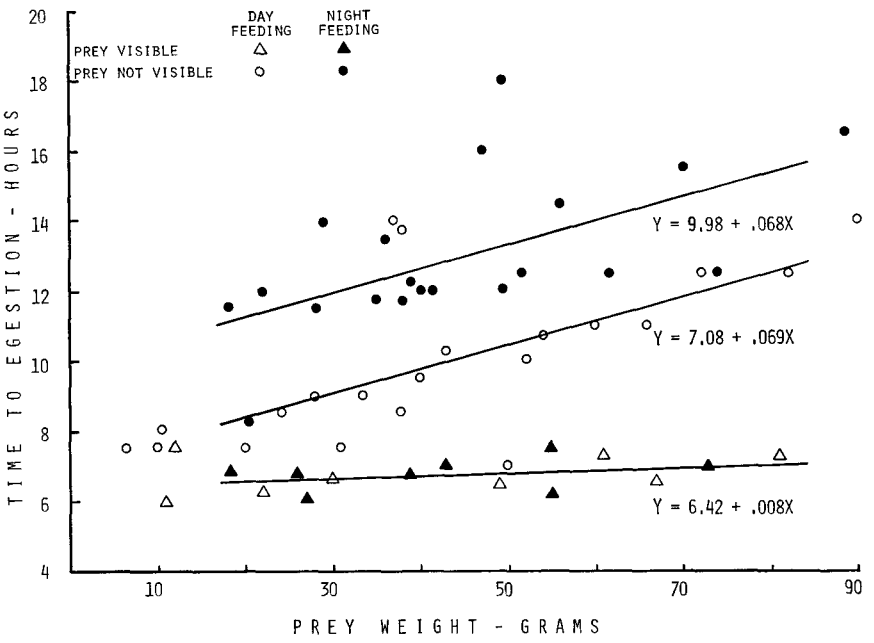

FIG. 3. The effects of feeding time, prey weight and visible prey on pellet egestion in the Barn Owl.

06:00 and 14:00 were arbitrarily grouped as "day feedings," while feedings from 16:00 until 24:00 were considered "night feedings." Figure 3 illustrates the effects of both time of feeding and food weight on the subsequent egestion of a pellet. The Y intercepts of the two lines (day = 7.08, night = 9.98) are different, showing that time between feeding and pellet egestion is longer at night than during the day. The calculated slopes from day and night feedings are significantly different from zero ($P \leqslant 0.05$) but not different from each other, pointing out that increasing prey weight delayed pellet egestion in the experimental owl regardless of time of feeding. Similar observations have been reported for the Short-eared Owl (*Asio flammeus*) (Chitty, 1938).

The Great Horned Owl (Reed, 1925) and the Tawny and Short-eared Owls (Chitty, 1938) have been observed to egest a pellet when presented with another food item. Guérin (1928) reported a similar phenomenon in the Barn Owl in Europe, and Reed (1897) observed a similar reaction in American Barn Owls. Our Barn Owl could be induced to egest a pellet simply by allowing it to see a live vole after a sufficient time had elapsed since the last feeding.

In order to examine the degree of influence of excess available prey on the normal pattern of pellet egestion, the bird was fed a prey item of known weight after which a wire cage containing additional live prey was placed in view of the bird. The owl could be observed from outside the room and as soon as the pellet was egested, the bird was given another weighed meal. This was continued with different size prey during both day and night periods until the owl killed and stored the prey instead of eating it. A total of 16 food-induced pellets, obtained in this manner, provided the data for the bottom line in Figure 3 which indicates that no difference in time until pellet egestion exists between day and night feedings when the owl is aware of the possibility of a subsequent meal. In addition, the slope from the pooled day-night feedings does not differ from zero even though prey weight varied from 10 to 81 grams. Since the stimulation provided by live prey was present during both day and night feedings, and since the prey consumed varied in weight from 10 to 81 grams, it is obvious that neither quantity consumed nor time of feeding delayed pellet egestion when a potential meal was in view.

The minimum time elapsing before the owl could be induced to egest a pellet by additional prey was about 6.5 hours ($Y = 6.42$ hours). A few pellets have been recovered under unusual circumstances in less time but the normal pattern for the bird is to continue eating prey when available prior to the 6.5-hour critical period and then form one large pellet which is egested long after the first meal was taken. Guérin (1928) also showed that subsequent feeding delayed pellet egestion in the Barn Owl. Few of our data relate to this, but the indication is that mice swallowed at intervals of less than 6 hours act to delay pellet egestion until the last prey item is digested. Obviously, this delaying effect has limits governed by the bird's capacity, but on several occasions two, three, and four mice have been consumed over an 8-hour period and all have been incorporated into a single pellet. Likewise, it is not unusual to find four, five, and even six *Microtus* skulls in a single Barn Owl pellet collected at a roost. Such instances are probably the result of continuous food intake with the intervals between successive meals never exceeding the critical 6.5-hour period after which a pellet would be formed and could be egested in response to the detection of a potential prey item.

Since pellet egestion can be prey-induced but is normally delayed when capture intervals are short, a bird completing a successful night of hunting would require the daylight hours to digest the mass of food it had collected. In the case of either a successful night of hunting or a poor night during which no mice were caught late enough to stimulate pellet egestion, the pellet formed and egested at the day roost would contain remains of everything the bird had consumed. The factors which determine the length of time that a pellet will be retained are (1) the length of time since the last food was consumed,

which in this study was at least 6.5 hours, and (2) the detection or capture of a prey item by the bird. Chitty (1938) suggested that hunger determines the length of time that a pellet is retained in the digestive tract before egestion. Hunger, however, would be a direct consequence of the bird not having prey available. In the absence of prey the pellet would be retained, not as a result of hunger, but as a result of a lack of the proper stimulus (available prey) for pellet egestion. This does not mean that egestion cannot occur in the absence of a stimulus but clearly it is delayed in such instances.

It is reasonable to assume, then, that most of the pellets collected at the roost site of a wild Barn Owl represent one successful night of hunting for each pellet. The possible exception to this would be those pellets egested on the feeding ground on a night of hunting during which only two or three mice were caught, with a period of 7 to 8 hours between any two successive captures (e.g., during a long winter night). In such a situation, a pellet would probably be egested away from the roost site, as suggested by Craighead and Craighead (1956) and reported by Guérin (1928). The egestion of such a pellet would be triggered by the last mouse caught. The pellet egested the next day, however, would still represent as much as half of the previous night's catch. One could judge the possibility of such an occurrence by determining the owl's hunting success as indicated by the number of prey items in each of the pellets collected at the roost. Small pellets containing only one prey item would be indicative of egestion away from the roost site and detract from the reliability of making judgments about food consumption from roost pellet collections.

SUMMARY

The factors influencing rates of pellet formation and egestion were studied in a Barn Owl kept in captivity for 6 months. The pH of the gastric contents changes according to a regular pattern from feeding until pellet egestion, but it could not be implicated definitely as a mechanism that triggers actual egestion. Data on gastric pH demonstrate the presence of a cephalic phase of digestion. The pellet is formed in the gizzard within 6 hours after ingesting a meal, and is passed into the proventriculus where it is held until egestion. Pellets are not egested at a fixed interval after taking a meal; the interval is dependent in part upon quantity of food consumed, time of feeding and availability of a subsequent meal. Increased prey weight and night feedings prolong the time to egestion but have no effect when a subsequent meal is available.

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DEPARTMENT OF BIOLOGY, EAST TENNESSEE STATE UNIVERSITY, JOHNSON CITY, TENNESSEE (PRESENT ADDRESS: NEW YORK COOPERATIVE WILDLIFE RESEARCH UNIT, CORNELL UNIVERSITY, ITHACA, NEW YORK 14850) AND BUREAU OF SPORT FISHERIES AND WILDLIFE, CORNELL UNIVERSITY, ITHACA, NEW YORK 14850, 24 JULY 1971.