GASTRIC EMPTYING AND GASTROINTESTINAL MOTILITY IN LEACH'S STORM-PETREL CHICKS (OCEANODROMA LEUCHORHOA)

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ABSTRACT.—We used radiographic techniques to observe gastric motility during digestion of a meal in four Leach's Storm-Petrel chicks, 40–55 days old. A radio-opaque substance was added to the daily feeding for radiographic observation. We observed a biphasic gizzard contraction cycle with a frequency of 7.5 cycles/min. Gastric emptying occurred with each cycle and frequent intestinal refluxes were observed. Proventricular contractions were rarely observed; when observed, they affected only the ventral surface near the gizzard. Layering of proventricular contents, which we assumed to be a layer of dietary lipid over an aqueous phase, developed postprandially. Limited proventricular motility would favor layering; and ventral proventricular motility, along with regular gizzard motility, would promote gastric emptying of the more ventral aqueous layer. These observations are consistent with the idea that procellariiform "stomach oils" are of dietary origin and that lipid accumulation in the stomach is linked to a unique gastrointestinal anatomy and motility. *Received 21 March 1988, accepted 22 August 1988.*

PROCELLARIIFORM birds (albatrosses, fulmars, shearwaters, and other petrels) can store oil in their large, glandular and distensible fore-gut or proventriculus. The oil is found in both chicks and adults (Lewis 1966, Grubb 1971) and in birds captured at sea or on land. The oil was originally thought to be from the preen gland (Carter and Malcom 1927) or proventricular secretions (Matthews 1949), but is now considered to be of dietary origin (Imber 1976, Clarke and Prince 1976, Warham 1977, Jacob 1982).

Cheah and Hansen (1970) proposed a mechanism for stomach oil formation in which low proventricular pH led to rapid breakdown of proteins and slow lipolysis, causing lipids to separate from the aqueous phase and accumulate. The heavy, more aqueous material settled and emptied first, followed by the lighter, oily lipid (Cheah and Hanson 1970, Warham 1977). This mechanism presumes that there is substantial layering of a lipid phase above an aqueous phase prior to proventricular emptying, and that the proventriculus must have limited gastric motility in order for the layering to persist. In humans, lipids empty from the stomach more slowly ($14 \pm 3\%$ h^{-1}) than aqueous ($34.3 \pm 1.8\%$ h^{-1}) or solid components ($22 \pm 1.8\%$ h^{-1}) (Jian et al. 1982), and some layering of lipids above nonlipids is found (Chang et al.

1968, Meyer et al. 1986). In birds, there are few studies that compare gastric emptying of lipid and aqueous components (Duke 1986a).

Our objective was to describe for the gastric motility in a representative procellariiform. We specifically examined whether lipid accumulated above an aqueous phase in the proventriculus and whether a lack of motility in the proventriculus accounted for accumulation of "stomach oils." We chose Leach's Storm-Petrel chicks (*Oceanodroma leucorhoa*) as our representative procellariiform. The diet of Leach's Storm-Petrel chicks has a high (up to 60% of fresh mass) lipid content (Place and Roby 1986). We fed meals containing $BaSO_4$ to storm-petrel chicks, and observed and recorded gastric motility cineradiographically. The observed gastric motility was considerably different than that previously described for other birds (Duke in press) and consistent with the accumulation of stomach oils in this species.

METHODS

Birds, food and feeding, and housing.—We obtained 4 juvenile Leach's Storm-Petrels of known hatch date from nesting burrows on Little Duck Island, Maine, on 25 August 1987. They were 39 days old on this date and their mass was 48–60 g (mean was 57 g).

Two of the nestlings died: one, on 1 September of an apparent respiratory problem; the other, on 8 September of an unknown cause. The remaining 2 birds were returned to Little Duck Island on 10 September and released on 15 September at the age of 60 days. Both chicks fledged successfully.

The birds were fed daily at 0730 an amount approximating 15% of their body mass. The diet consisted of freeze-dried copepods (predominantly *Limnoclanus macrurus*, 87% of the biomass), water, and olive oil. We homogenized the copepods and water (mixed 1:4, respectively) in a blender; then we added the homogenate to olive oil in the proportions 2 to 1. This mixture was delivered directly into the proventriculus via stomach tube. Birds were housed in a heavy, waxed cardboard box (44 × 30 cm), divided into 4 chambers (22 × 15 cm each). Their holding room was held at 14°C in constant darkness which simulated conditions in their nest burrows (Place and Roby 1986).

Radiographic procedures.—We conducted radiographic observations via image intensification radiology (Phillips Super M100, Phillips Medical Systems, Inc., Shelton, Connecticut; e.g. Dziuk and Duke 1972, Rhoades and Duke 1975, Chaplin et al. 1987) which permitted viewing of the radiographic image on a video monitor and recording on videocassettes. Approximately 100 min of videotape was obtained for subsequent study. Figures herein are photographs taken from the video monitor while the videotape was "paused." Starting immediately after feeding, we made radiographic observations from 0730–0930 and 1130–1330 on 4 days, and from 1530–1730 on 2 days, for a total of 20 hours.

Chambers of similar size to those in which the birds were housed were constructed of cardboard with one chamber above the other. Thus, unless the 2 subjects moved to opposite ends of their respective chambers, 2 birds could be studied simultaneously. Generally, our observations were made in lateral view, but both cranio-caudal and caudal-cranial views were also possible when a bird turned perpendicular to the long axis of its chamber.

In order to visualize the shape, or changes in shape, of the lumen of the GI tract, a $BaSO_4$ solution (Liquid Polibar E-Z-EM Co. Inc., Westbury, New York) was added to the food. The concentration of this solution was varied to determine which concentration gave the best contrast. In this study the best concentration proved to be a 10% solution of $BaSO_4$ (on a volume basis). Two cc of the commercial $BaSO_4$ suspension ($1BaSO_4:2H_2O$ by mass) were added to 8 cc of the food mix and shaken gently for 15–30 s to disperse it into the food. We determined how well this suspension "labeled" the various constituents of our petrel diet by adding 10 cc of the suspension to 40 cc of water, olive oil, or to the prepared diet. These mixtures were shaken gently then set in a water bath at 40°C and observed for 2 h.
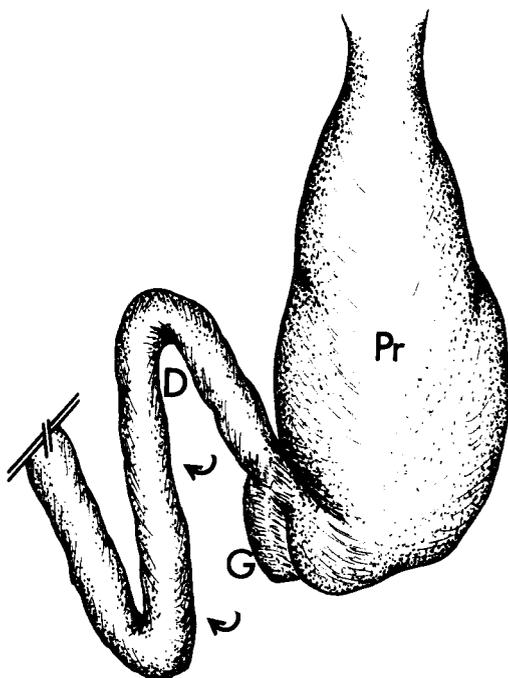

Fig. 1. Ventral view of the visceral mass in a young Leach's Storm-Petrel (*Oceanodroma leucorhoa*) with the liver removed. Pr = proventriculus; G = gizzard; D = duodenum. Arrows indicate that the duodenum was shifted to expose the gizzard.

RESULTS

The proventriculus of Leach's Storm-Petrel is large and fills approximately half of the caudal thoracoabdominal space when fully distended with a meal. The gizzard is considerably smaller and is somewhat disc-shaped (Fig. 1). The long axis of the disc is oriented dorsoventrally and is attached at a point on its circumference to the ventromedial surface of the proventriculus.

After a feeding containing $BaSO_4$, the dominant radiographic image was the proventricular lumen (Fig. 2). A comparison of the relative size and position of the proventriculus in a dead specimen to the radiographic image of the proventricular lumen indicated that the proventriculus became distended primarily in the caudal direction after feeding. We could also see the lumen of some coils of the small intestine usually within 30–45 min postprandially (Fig. 2). Gastric emptying appeared to begin immediately after feeding. We could not see the lumen of the gizzard in lateral view unless a bird was slightly tipped with one side higher off the
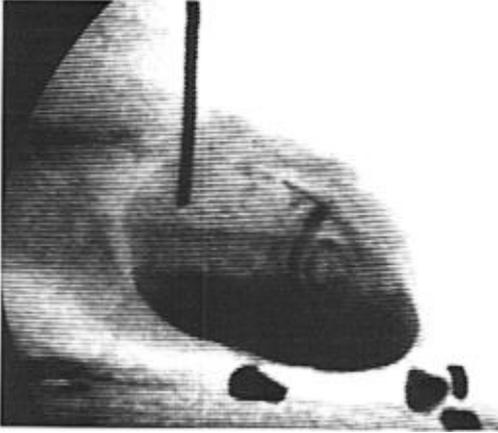
Fig. 2.   Lateral radiographic image of the abdomen of a Leach's Storm-Petrel at ca. 2 h postprandially; caudal is on the right. The large, egg-shaped image filling most of the abdominal area is the proventriculus. Three layers of radio-opacity are evident; the pointer indicates the boundary between the upper two layers. Coils of small intestine filled with BaSO₄ appear in the caudal portion of the abdomen. Irregular shapes below the proventriculus are excreta containing BaSO₄.

Fig. 3.   Radiographic image of the proventriculus partially filled with BaSO₄ at ca. 6 h postprandially. Some layering is evident as is a contraction (indentation) of the ventral surface.

floor of the chamber than the other. Fortunately, the birds frequently assumed this position while preening back and tail feathers. In addition, the chamber could be tipped slightly to expose the shape of the gizzard lumen as it contracted.

The proventriculus contracted infrequently during our radiographic observations. Contractions involved only the ventral surface (Fig. 3). Occasionally, contractions appeared to move from the caudal margin of the proventriculus towards the gizzard (i.e. peristalsis-like), but most contractions did not move.

The contraction of the gizzard was biphasic and began with the cranial and caudal margins moving medially. This contraction produced a roughly square radiographic image (Fig. 4 [middle], phase I). The contraction of the cranial margin was less vigorous than that of the caudal, presumably because movement of the cranial margin is restricted by its attachment to the proventriculus and duodenum (Fig. 1). Following relaxation of the cranial and caudal margins, the dorsal and ventral margins contracted to produce a rectangular image on the radiograph (Fig. 4 [bottom], phase II). The frequency of this biphasic contraction cycle in the gizzard was 7.5 contractions/min.
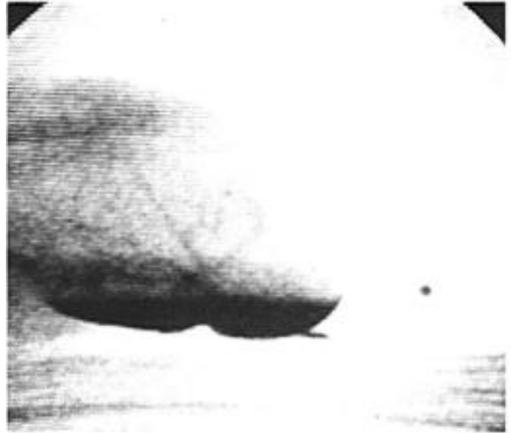
On one occasion, a repeated series of small contractions (shallow indentations of the lumenal outline) was observed moving along the ventral margin of the proventriculus. Each contraction began as the first phase of the gizzard contraction started and ended upon reaching the gizzard at approximately the end of the second phase of the gizzard contraction. This was our only observation of coordinated motility between the proventriculus and gizzard.

As indicated above, gastric emptying began immediately after feeding. Duodenal outflow occurred immediately after the first phase of the gizzard contraction and some outflow occurred with nearly every gizzard contraction cycle. The BaSO₄-food mixture moved rapidly through the intestine, sometimes filling the length of the duodenum or a coil of intestine (Fig. 4) in 2–3 s. Presumably peristalsis accounted for these movements but, because of the small size of the intestine and the rate of movement of the BaSO₄ image, we could not see intestinal contractions. In addition to aborad flux, orad refluxes also occurred frequently. Because we concentrated on gastric motility, we did not determine precisely the frequency of the intestinal refluxes. Their approximate frequency was 5–6 waves/h for the jejuno-ileal segment and perhaps twice that rate in the duodenum.

As gastric emptying progressed postprandially, we observed a layering of proventricular contents (Fig. 2). This layering presumably represented a separation into aqueous and lipid components. The aqueous layer contained more
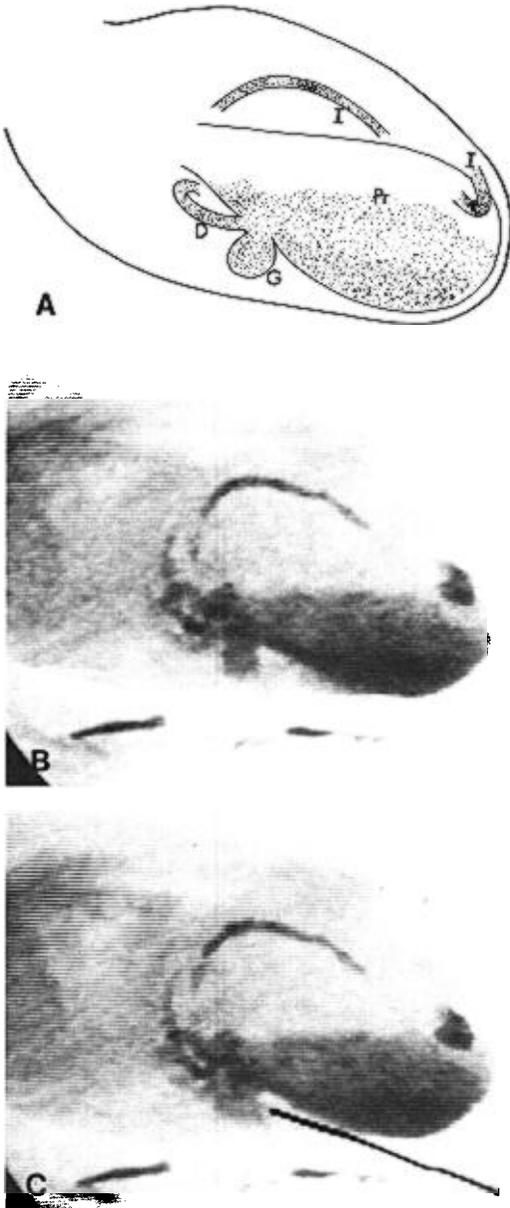
A

B

C

Fig. 4.   Top: Drawing of radiographic images shown in Middle and Bottom. Pr = proventriculus; G = gizzard; D = duodenum; I = small intestine. Middle: Radiographic image of the first phase of gizzard contraction, i.e. contraction of cranial and caudal margins. Bottom: Radiographic image of the second phase of gizzard contraction involving the dorsal and ventral margins.
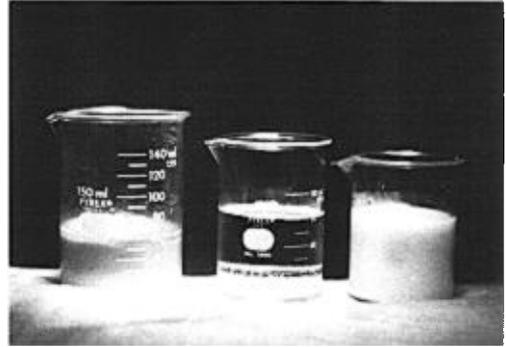

Fig. 5.   Left: Beaker with Leach's Storm-Petrel meal mixed with $BaSO_4$. The density of $BaSO_4$ increased nearer the bottom of the suspension. Middle: Beaker with olive oil and $BaSO_4$. $BaSO_4$ has settled to the bottom. Right: Beaker with water mixed with $BaSO_4$. $BaSO_4$ is suspended evenly throughout mixture. The photograph was taken 2 h after making the three suspensions.

$BaSO_4$ than the lipid layer. We tested for this layering in vitro by adding a commercial $BaSO_4$ suspension to water, olive oil, or a meal. The suspension remained evenly distributed in water for the 2 h of observations (Fig. 5). It settled to the bottom of the beaker containing olive oil in 30–45 min. In the meal suspension the lipid had begun to separate during the 2-h trial and a very thin layer of water had settled to the bottom of the beaker. This water layer was heavily labeled with the $BaSO_4$ suspension. In the mixture above the water layer, a gradient of $BaSO_4$ density was evident with greatest density immediately above the water layer and least density farther from the water (Fig. 5).

DISCUSSION

The gross anatomy of the gastrointestinal tract of Leach's Storm-Petrel is identical to that of the British Storm-Petrel (*Hydrobates pelagicus;* Matthews 1949). In both species, the proventriculus is an enormously long, thin-walled organ which extends to the caudal end of the abdominal cavity before bending cranially and then medially to join the relatively small gizzard. Because the opening to the duodenum is on the dorsolateral side of the gizzard the proximal portion of the duodenum first ascends before forming the typical duodenal loop enclosing the pancreas. The gross anatomy of Leach's Storm-Petrel's gizzard is similar to that of raptors (Duke 1985) and Ardeidae (Rhoades and

Duke 1975), which are also carnivores. This gizzard lacks the opposing pairs of thin and thick muscles characteristic of fowl and most other avian species (Duke 1986a). The gizzard is, however, much smaller than that of raptors or other species and the proventriculus is much larger (Matthews 1949, McLelland 1979). The gizzard of a Great Horned Owl (*Bubo virginianus*) is approximately twice the size of the proventriculus (Duke 1985), whereas the gizzard of a Leach's Storm-Petrel is perhaps $\frac{1}{20}$ the size of the proventriculus. The enlarged proventriculus is characteristic of procellariiform birds and only a few other bird species (McLelland 1979). The apparent function of the proventriculus in the Procellariiformes (chemical digestion of ingesta) is also unique. In most other species, food quickly passes through the proventriculus and both chemical and mechanical digestion occurs in the gizzard (Duke 1986b). The contraction pattern of the procellariiform gizzard, as seen radiographically, appears to be very similar to that of fowl. Contraction of the cranial and caudal thin muscles of the gizzard produced a somewhat square image when viewed radiographically (as seen in Fig. 4 [middle] for Leach's Storm-Petrel, phase I). This phase of the cycle was followed by contraction of the dorsal and ventral thick muscles which produces a more elongate or rectangular image (like Fig. 4 [bottom], phase II) (Dziuk and Duke 1972). Duodenal emptying occurs between the two phases in fowl as it does in Leach's Storm-Petrel.

The contraction frequency of the procellariiform gizzard is approximately twice that of fowl (Duke 1986a) and five times that of raptors (Kostuch and Duke 1977). The contraction frequency of the procellariiform proventriculus is much less than that of other species because the proventriculus appears to be relatively inactive in petrels. There is insufficient data to determine whether gizzard contraction frequency in birds is allometric with body mass. Great Horned Owls are intermediate in body size between chickens and turkeys (each exhibiting 3 contractions/min) but have a gizzard contraction frequency one-half of fowl (Duke 1986a). Characteristic of both raptors and fowl is a regular gastroduodenal contraction sequence that involves the proventriculus, gizzard, and duodenum (Duke in press). We observed coordination of proventriculus and gizzard motility only once. Gizzard and duodenal coordination exists because emptying into the duodenum usually occurred with each giz-

zard contraction cycle. Intestinal refluxes occur approximately three times more often in Leach's Storm-Petrel than in fowl. This may be related to the relatively larger amount of lipid hydrolysis in the intestine required by the higher fat content diet (Place and Roby 1986) as compared to commercial poultry rations.

A process which allows accumulation of lipids in the proventriculus can be readily deduced from our results. Avian proventricular secretions would be expected to include only water, mucus, HCl and pepsin (Duke 1986b). Proventricular pH's of 2.57 ± 0.5 have been recorded in Leach's Storm-Petrel chicks (Place et al. 1986), and there is little or no lipolysis in the proventriculus (Hewitt and Schelkopf 1955, Roby et al. 1986, Place and Roby 1986). Cheah and Hanson (1970) and Warham (1977) hypothesized that proteins would be degraded rapidly in this environment while lipids would not be, and the less dense lipids would likely form a layer over the aqueous, proteinaceous layer. Proventricular contractions occur only along the ventral surface and contents near the surface (i.e. the aqueous phase) would empty from the proventriculus first. As much as 6.63 ± 1.15 ml of an isotonic glucose solution can empty from the proventriculus within 1 h after feeding (Place et al. 1986). Vigorous contractions of the gizzard would "pump" these contents into the intestines. The substance would most likely be low in lipids, including only polar lipids such as phospholipids and fatty acids in the aqueous layer and possibly a few lipids from the interface between the aqueous and lipid layers. Presumably, once the proteinaceous ingesta have left the proventriculus, emptying would continue but at a slower rate. The presence of lipids in the duodenum slows gastric emptying in turkeys (Duke and Evanson 1972). Subsequent meals would add additional lipid to that accumulated from prior meals, and provide an energy and metabolic water reserve during periods when the chicks are not fed (Warham 1977).

We believe the unique aspects of gut morphology and motility in Leach's Storm-Petrel chicks are appropriate to their high-fat diet and are responsible for the accumulation of stomach oils in birds of the Order Procellariiformes.

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