winged Blackbirds in central North America. Univ. Kansas Publ. Mus. Nat. Hist. 19:1–83.

RITCHISON, G. 1983. The function of singing in female Black-headed Grosbeaks (*Pheucticus melanocephalus*): Family-group maintenance. Auk 100: 105–116.

SEARCY, W. A. 1979. Male characteristics and pairing success in Red-winged Blackbirds. Auk 96:353–363.

SEARCY, W. A. 1988. Do female Red-winged Blackbirds limit their own breeding densities? Ecology 69:85–95.

SEARCY, W. A. 1989a. Function of male courtship vocalizations in Red-winged Blackbirds. Behav. Ecol. Sociobiol. 24:325–331.

SEARCY, W. A. 1989b. Dual intersexual and intrasexual functions of song in Red-winged Blackbirds. Pages 1373–1381 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.

YASUKAWA, K. 1981. Song and territorial defense in the Red-winged Blackbird. Auk 98:185–187.

Received 4 November 1991, accepted 15 June 1992.

The Auk 109(4):933–936, 1992

Intestinal Transit: How Can It Be Delayed Long Enough for Birds to Act as Long-distance Dispersal Agents?

MARY H. CLENCH AND JOHN R. MATHIAS
Division of Gastroenterology, Department of Internal Medicine,
The University of Texas Medical Branch, Galveston, Texas 77555, USA

We recently described the rhythmic oscillating complex (ROC), a myoelectric/motor complex in avian small intestine (Clench et al. 1986, Clench and Mathias 1992). Because the gastrointestinal tract resumes fed-state motor activity after a ROC has occurred, we suggested that this motor event functions to recycle the small amount of food remaining in the gut of a bird that has been unable to continue feeding. In addition to its physiological importance, such a mechanism has ecological implications, especially in regard to how birds may disperse the propagules of other organisms.

In brief, we demonstrated in galliforms that after an individual has undergone a long fast and the proximal gut has emptied of food and become quiescent, ROCs begin to occur (Clench and Mathias 1992). The complex consists of rapidly moving bursts of spike potentials/ring contractions that propagate in alternating directions, orad and aborad—apparently a back-and-forth stripping motion that travels the entire length of the small intestine. ROC activity is prolonged, continuing for a mean of 7.6 min in chickens (*Gallus gallus*) and 15.4 min in a Ring-necked Pheasant (*Phasianus colchicus*). After a ROC has ended, fed-state motor activity resumes in the stomach and small intestine, indicating that food has been moved into the proximal tract for further digestion and absorption—seemingly recycled, probably from the distal part of the tract. As a bird continues to fast, ROCs also continue to occur periodically. How often the complex occurs is individually variable, but it is no more frequent than every 3 h and the intervals are often much longer. With each ROC, the distal gut is restimulated into fed-state activity that lasts for shorter and shorter periods. A reasonable conclusion from this last observation is that in a long-fasting bird, after each successive ROC, less and less food remains in the tract to be recycled and thus the fed-state activity restimulated by the complex gradually diminishes.

The length of time required for food to move through the avian digestive tract ("transit time") has been measured in many species by using nondigestible, nonabsorbable physical markers or radioactive tracers (Duke 1986). Although many variables must be considered, food passage in birds is generally rapid compared with that of mammals (especially ruminants) or other vertebrates (c.f. data in Warner 1981, Karasov et al. 1986). For example, studies have shown that color-marked barium sulfate required only 22.9 to 69.4 min to move through the gut of passerines, based on data from about 700 individuals of more than 30 species (Herrera 1984, Jordano 1987). Although some of those measured transit times could have been unnaturally fast because barium ions stimulate intestinal tissue (Burnstock and Holman 1966, Daniel 1968), Herrera (1984) noted that fruit passage times he also recorded in some of the birds were often faster than those of the barium.

Some frugivorous species have been shown to have particularly rapid transit. Holthuijzen and Adkisson (1984) timed the passage of red cedar (*Juniperus virginiana*) cones and flowering dogwood (*Cornus florida*) fruits through fasted Cedar Waxwings (*Bombycilla cedrorum*) at means of 11.7 and 22.9 min, respectively. Walsberg's (1975) elegant study of Phainopeplas (*Phainopepla nitens*) demonstrated that desert mistletoe

(*Phoradendron californicum*) berries, to which the species is highly adapted, passed through a bird in 12 to 45 min ($\bar{x}$ = 29 min). If Phainopeplas have an intestinal length of 13 cm (measured from Walsberg's published figure), a rough estimate of 0.5 cm/min can be calculated for their mean transit rate. If waxwings have an intestine 15 cm long (also measured from Walsberg 1975), their transit can be estimated at 0.8 and 1.5 cm/min for the two test foods used by Holthuijzen and Adkisson (1984).

Because flightless species could be considered free of evolutionary constraints against carrying heavy loads of food in the body, they might be expected to have slower transit rates than would a volant species eating the same diet. When Laugksch and Duffy (1986) measured dye recovery from injected fish meals in Jackass Penguins (*Spheniscus demersus*) and Cape Gannets (*Sula capensis*), a mean of 21.1 h was required for 95% of the dye to pass through the penguins and 22.1 h to pass through the gannets. In a less sophisticated experiment, Honigmann (1936) reported 22 h for Jackass Penguins. When discussing the apparently slow transit of these birds, however, Laugksch and Duffy (1986) did not consider the potential effect of the relative lengths of the species' digestive tracts, or the fact that piscivorous species have comparatively long intestines (data from Mitchell 1901). Intestinal length of Cape Gannets has not been measured, but Beddard (1898) reported a length of 1.5 m (small plus large intestine) in a related species, the Northern Gannet (*Sula bassanus*). Magellanic Penguins (*Spheniscus magellanicus*) have an intestine that is seven times longer—10.5 m (Beddard 1898). The illustrations of *demursus* and *bassanus* in Mitchell (1901) also show that penguins have a comparatively much longer gut than do gannets. Thus, assuming that related species have similar gut lengths (when being measured grossly, in meters), the extreme distance that food had to traverse in a penguin in slightly less than a day implies a rapid transit rate in a flightless bird: roughly estimated here at 0.8 cm/min in penguins vs. 0.1 cm/min in gannets. Interestingly, the transit rate of the long-gutted piscivorous penguin appears to be in the same general range as rates of the short-gutted frugivorous waxwing and Phainopepla.

Characteristics of the food consumed also affect the speeds at which food is moved through the gut as it is digested and absorbed, and as the nondigestible portions are passed down the tract. Duke (1986) listed factors, such as consistency, hardness, water content, and nutrient (especially fat) composition, that have been shown to affect transit time. Certain diseases are also known to depress digestive function, as are environmental influences such as high temperatures (Duke 1986). In general, however, the normal passage of food through a bird is a relatively fast process, in most cases from a few minutes to about 12 h.

Despite the rapid transit, assimilation efficiencies are relatively high in birds—a mean of 74% to 78% for most foods (seeds, invertebrates, meat, fish, or artificial diets) regardless of avian taxon (Castro et al. 1989). Assimilation efficiency increases with fat content and decreases with very high protein levels (Castro et al. 1989), and retention times usually vary directly with nutritional levels (Halse 1984). Interestingly, lipids slow intestinal motility (e.g. Duke and Evanson 1972, Roby et al. 1989).

It is well documented that birds have an important ecological function as long-distance dispersal vectors for biological propagules: seeds, spores, bacteria, fungi, protozoa, plankton, nematodes and other worms, subadult stages of insects, plankton, and various other microorganisms (e.g. Malone 1965, Proctor 1968, Herrera 1984, Suthers 1985 and references therein). But considering the generally rapid avian transit times, it is difficult to understand how these propagules can be retained in a bird's gut long enough to be carried meaningful distances. This problem has not been addressed.

In some species, ingesta can be held in the proximal end of the digestive tract, in a crop or esophageal diverticulum, for various lengths of time before entering the stomach/intestine (White and Stiles 1990). The distal tract can also hold ingesta in species with functional ceca; liquids, including marker dyes, and fine particles of a digested test meal may be diverted after passing through the small intestine and be defecated much later from the ceca (Duke et al. 1968). These are not, however, the only possible mechanisms for delayed passage of food; the ROC offers another explanation.

If the more readily digested parts of a meal have already cleared the stomach and intestine, but undigested materials such as hard seeds are still present in the tract, they could be repeatedly shunted to the proximal gut by ROC action. Typical results of studies using food markers show that with any given meal, some of the marker being used to measure transit appears relatively rapidly, most is gradually but steadily recovered, and the last marker may be retained for a long time. For instance, in Willson's (1989) study, 10% or fewer of the solid markers (pseudoseeds—polyester buttons and nylon beads) embedded in apple and fed to Emus (*Dromaius novaehollandiae*) emerged the first day. The first pseudoseeds appeared in 4 h, which represents a transit rate of 1.5 cm/min in Emus (intestinal length, 3.5 m; Beddard 1898). Yet, it required 2 days for about 75% of the markers to appear, and the last were retained for as long as 10 days. A recycling motor event that is activated when the gut has almost emptied, especially at night when birds are not feeding and enter a fasting state, could account for the extended transit typically experienced with the last part of a meal in Emus and many other species.

Repeated recycling by ROCs would tend to break down some food items more thoroughly than others, but hard natural seeds have been recovered from avian gut after long transit periods. Viable seeds have been recovered from the feces of ducks, geese, quail, pigeons, and jays 24 h or more after ingestion, enough time for a migratory flight and potential long-distance seed dispersal (Proctor 1968). Viable regurgitated seeds of *Rhus glabra* have also been recovered after they were in the digestive tract of a Killdeer (*Charadrius vociferus*) more than 14 days (Proctor 1968). We believe, however, that simple lodging of food items in the crop, stomach, or other gut diverticula cannot account for all the delayed transit that has been reported.

To date, the ROC has been demonstrated in three gallinaceous species: chickens and Ring-necked Pheasants (Clench and Mathias 1992); and turkeys (*Meleagris gallopavo*; G. E. Duke pers. comm.). We have failed to elicit the complex in Barred Owls (*Strix varia*). Preliminary evidence in chickens (Clench and Mathias 1992) suggests that the ceca are the most reasonable source of nutrients for ROC recycling. Galliforms and many other birds have an intestinal type of ceca that has multiple functions, including digestion of food (Ziswiler and Farner 1972). The ceca of owls and a few other birds (rails, *Amaurornis* and rollers, *Coracias*) are of a different histological type and apparently are limited to secretion (Naik 1962). Thus, if a ROC recycles food and if the ceca are involved in that recycling, one might expect that galliforms and other species with functional intestinal ceca would have the complex, but that a Barred Owl would not.

Our recycling hypothesis not only offers an explanation of how birds may digest food more completely on one occasion than on another, but it also means that calculations of food assimilation efficiencies must include the length of time that experimental birds have been deprived of food (Castro et al. 1989 and references therein). When food is not readily available in the environment, or when preferred food items are scarce or absent, birds might feed less often, thus repeatedly entering the fasted state between feedings. Under these circumstances, if refluxing and recycling occurs proportionately more often per unit of food consumed, a food-deprived bird could be shown to digest its meals more thoroughly than when food was abundant. Certainly, birds are well known to assimilate certain foods better than others (e.g. Castro et al. 1989, Levey and Karasov 1989), and hungry birds have been shown to prolong digestion time as well as increase thoroughness of digestion. Duke et al. (1980) demonstrated that hungry Barred Owls seemed to be able to prolong digestion time as well as increase the degree of digestion. Owls on a submaintenance diet had significantly longer meal-to-pellet intervals (therefore, held prey items in stomach longer) and the pellets weighed less (were more thoroughly digested) than when the same birds were on either a maintenance or above-maintenance diet. In addition, these reactions increased the longer the birds were held on short rations. Because the present study did not elict ROCs in Barred Owls, we presume this species accomplishes food retention in the stomach, not through intestinal recycling.

The emphasis in ornithology in recent years has been on how a bird acquires its food (resource partitioning, etc.). Clearly, however, there is also a great deal more to be learned about what happens within that bird *after* it has fed.

We are grateful to Gary E. Duke, Douglas J. Levey, and an anonymous reviewer, whose thoughtful comments on the first draft of this paper greatly improved the final version.

LITERATURE CITED

BEDDARD, F. E. 1898. The structure and classification of birds. Longmans, Green, London.

BURNSTOCK, G., AND M. E. HOLMAN. 1966. Effect of drugs on smooth muscle. Pharmacol. Rev. 6:129–156.

CASTRO, G., S. STOYAN, AND J. P. MYERS. 1989. Assimilation efficiency in birds: A function of taxon or food type? Comp. Biochem. Physiol. A Comp. Physiol. 92A:271–278.

CLENCH, M. H., AND J. R. MATHIAS. 1992. A complex avian intestinal motility response to fasting. Am. J. Physiol. 262:G498–G504.

CLENCH, M. H., V. M. PIÑEIRO-CARRERO, R. H. DAVIS, AND J. R. MATHIAS. 1986. Rhythmic oscillating complex: Intestinal motor response to prolonged fasting in nonmammalian vertebrates (Abstract). Gastroenterology 90:1387.

DANIEL, E. E. 1968. Pharmacology of the gastrointestinal tract. Pages 2267–2324 *in* Handbook of physiology. Section 6, Alimentary canal. Vol. 4, Motility (C. F. Code, Ed.). American Physiological Society, Washington, D. C.

DUKE, G. E. 1986. Alimentary canal: Anatomy, regulation of feeding, and motility. Pages 269–288 *in* Avian physiology, 4th ed. (P. D. Sturkie, Ed.). Springer-Verlag, New York.

DUKE, G. E., AND O. A. EVANSON. 1972. Inhibition of gastric motility by duodenal contents in turkeys. Poultry Sci. 51:1625–1636.

DUKE, G. E., M. R. FULLER, AND B. J. HUBERTY. 1980. The influence of hunger on meal to pellet intervals in Barred Owls. Comp. Biochem. Physiol. A Comp. Physiol. 66A:203–207.

DUKE, G. E., G. A. PETRIDES, AND R. K. RINGER. 1968. Chromium-51 in food metabolizability and passage rate studies with the Ring-necked Pheasant. Poultry Sci. 47:1356–1364.

HALSE, S. A. 1984. Food intake, digestive efficiency and retention time in Spur-winged Geese *Plectropterus gambensis*. S. Afr. J. Wildl. Res. 14:106–110.

HERRERA, C. M. 1984. Adaptation to frugivory of

Mediterranean avian seed dispersers. Ecology 65: 609-617.

HOLTHUIJZEN, A. M. A., AND C. S. ADKISSON. 1984. Passage rate, energetics, and utilization efficiency of the Cedar Waxwing. Wilson Bull. 96:680-684.

HONIGMANN, H. 1936. Studies on nutrition of mammals, part 1. Proc. Zool. Soc. Lond. 1936:517-530.

JORDANO, P. 1987. Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp. Ibis 129:175-189.

KARASOV, W. H., E. PETROSSIAN, L. ROSENBERG, AND J. M. DIAMOND. 1986. How do food passage rate and assimilation differ between herbivorous lizards and nonruminant mammals? J. Comp. Physiol. B Comp. Biochem. 156:599-609.

LAUGKSCH, R. C., AND D. C. DUFFY. 1986. Food transit rates in Cape Gannets and Jackass Penguins. Condor 88:117-119.

LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106:675-686.

MALONE, C. R. 1965. Dispersal of plankton: Rate of food passage in Mallard ducks. J. Wildl. Manage. 29:529-533.

MITCHELL, P. C. 1901. On the intestinal tract of birds. Trans. Linn. Soc. Lond., Zool. 8:173-275.

NAIK, D. R. 1962. A study of the intestinal ceca of some Indian birds. M.Sc. thesis, Banaras Hindu Univ., Varanasi, Uttar Pradesh, India (copy deposited in Section of Birds Library, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania).

PROCTOR, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160:321-322.

ROBY, D. D., K. L. BRINK, AND A. R. PLACE. 1989. Relative passage rates of lipid and aqueous digesta in the formation of stomach oils. Auk 106: 303-313.

SUTHERS, H. B. 1985. Ground-feeding migratory songbirds as cellular slime mold distribution vectors. Oecologia 65:526-530.

WALSBERG, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. Condor 77:169-174.

WARNER, A. C. I. 1981. Rate of passage of digesta through the gut of mammals and birds. Nutr. Abstr. Rev. Ser. B 51:789-821.

WHITE, D. W., AND E. W. STILES. 1990. Co-occurrences of foods in stomachs and feces of fruit-eating birds. Condor 92:291-303.

WILLSON, M. F. 1989. Gut retention times of experimental pseudoseeds by Emus. Biotropica 21:210-213.

ZISWILER, V., AND D. FARNER. 1972. Digestion and the digestive system. Pages 343-430 *in* Avian biology, vol. II (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

Received 2 October 1991, accepted 23 February 1992.

The Auk 109(4):936-937, 1992

The Insurance Hypothesis and the Theory of Clutch Size in Birds and in Invertebrates

I. C. W. HARDY
Department of Population Biology, University of Leiden,
P.O. Box 9516, 2300 RA, Leiden, The Netherlands

The theory of adaptive clutch sizes began with Lack's (1947) hypothesis, formulated for altricial birds, that selection maximizes the number of young produced per nest. In addition to stimulating a large and continuing amount of research on avian clutch sizes (e.g. Blackburn 1991, Rohwer 1991), these ideas have been successfully applied to invertebrate clutch sizes. This in itself has become a thriving research area (Godfray 1987). Regrettably, it seems that, although essentially the same, these research areas at times have become estranged (but see Godfray et al. 1991).

Power et al. (1989) offered the following explanation for European Starling (*Sturnus vulgaris*) clutch sizes smaller than would "normally" maximize fitness: conspecific brood parasitism (CBP; the adding of eggs to a clutch by conspecifics) can result in an overcrowded nest and a drastic reduction in fledgling success. As an insurance against the possibility of CBP, the starlings lay a smaller clutch, which on average is more productive than a "normal" clutch laid without anticipation of CBP. Rothstein (1990) reported the Power et al.'s hypothesis as novel, but in fact the idea is essentially the same as one developed originally for hymenopteran parasitoids by Parker and Courtney (1984). Superparasitism in parasitoids (van Alphen and Visser 1990), or more generally superoviposition (Godfray 1987) in invertebrates, is analogous to CBP in birds. Using an ESS model to consider the clutches sequentially laid on the same host by two conspecific parasitoids, Parker and Courtney showed that the clutch size produced by the first female should decrease as the probability of super oviposition increases. The prediction that the probability of superparasitism influences clutch size has