Long-Distance Dispersal of Seeds by Retention in Digestive Tract of Birds

Abstract. *Viable seeds of* Celtis, Convolvulus, Malva, *and* Rhus *were regurgitated from the digestive tract of killdeer* (Charadrius vociferus) *after 160, 144, 152, and 340 hours, respectively; seeds were recovered in the same way, after long-time retention, from least sandpipers* (Erolia minutilla). *Most other birds do not retain seeds as long. There is evidence that seeds of many species can remain viable in the intestinal tract of some shorebirds long enough to be transported several thousand miles.*

The suggestion that seeds may be transported via the digestive tract of migrating birds has been rejected (*1*) on the assumption that seeds were not retained very long in birds. Most writers (*1*), instead of examining the passage of seeds through birds, have assumed, on the basis of limited studies (*2*), that seeds were seldom retained more than 2 to 11 hours. Moreover, the 11-hour maximum was based on a cassowary, a bird unlikely to carry seeds long distances (*3*).

These figures may not apply to most migrants (*4, 5*). In fact, we found viable seeds of many aquatic plants in the digestive tracts of killdeer and mallard ducks after 24 to 48 hours, and in a few after more than 100 hours (*5*). We now report that some seeds can be retained even longer (200 to 300 hours), and we explain why some birds retain particular seeds much longer than other birds do.

Seeds of 13 common angiosperms (Table 1) were mixed with food or in gelatin capsules (*6*) and fed to 12 species of caged birds (*5, 7*) including shorebirds, upland species, migrants, and nonmigrants. We selected various seeds (*8*) in order to determine what size, shape, and composition could pass through the digestive tracts of the birds, and the maximum retention of such seeds.

Our results (Table 1) indicate that (i) many seeds can be retained for only 8 to 12 hours; (ii) some seeds, particularly those with a diameter greater than 1 mm and a hard seedcoat, may be retained for more than 100 hours; and (iii) most seeds may be retained by some charadriiforms for much longer than by any other birds examined.

Three factors probably cause the killdeer and least sandpipers to retain viable seeds so long: (i) much smaller seeds were retained in the gizzard by charadriiforms and columbiforms (italic numbers in Table 1) than by other birds examined; (ii) charadriiforms, unlike the two columbiforms, exerted relatively slight mechanical and enzymatic digestive action on seeds retained in the gizzard; and (iii) killdeer and least sandpiper, by contrast to many other birds (like lesser yellowlegs, jays, and ravens), did not regurgitate compacted, fibrous pellets from the gizzard, but only unconsolidated particles at irregular intervals.

Long-distance dispersal of seeds therefore occurs more frequently in migratory charadriiforms (because they do not regurgitate pellets) carrying hard seeds, 2 to 6 mm in diameter. Unfortunately, the regurgitation patterns of most birds, including charadriiforms, are unknown (*9*).

Most of the seeds we recovered from killdeer and least sandpipers were regurgitated, a few at a time, during the 24 hours immediately after ingestion. It took several days for the last three or four seeds to be regurgitated (*10*). The two western sandpipers (*Ereunetes mauri*) and one Wilson's phalerope (*Steganopus tricolor*) that we studied also regurgitated isolated particles rather than pellets from the gizzard.

We found, contrary to previous interpretations, that many seeds can be retained long enough to be transported to the most isolated oceanic islands. We now consider several other important objections (*1*) to the role of birds in the long-distance dispersal of seeds: (i) shorebirds do not ingest seeds; (ii) many long-distance migrants distribute mainly along coasts and not upland; and (iii) birds empty the digestive tract before migrating. Although most charadriiforms are predominately insectivorous or carnivorous, many may also eat and carry seeds for part of the year (*5, 11*). In fact, 37 gizzards of 90 killdeer collected in the vicinity of Lubbock, Texas, contained viable seeds, many from upland sites (*5*). One need not assume that seeds are transported from one land mass to another by one bird or one kind of bird. Many birds, including those that retain seeds for

Table 1. Maximum intervals (hours) between ingestion and recovery of last viable seed from the digestive tracts of birds. The number of birds used in each trial and on which maximums are based is in parentheses to the right of the common names. Seeds are listed in approximate order of size, with the smallest to the left of the table. Numbers in italic face refer to seeds retained in gizzard until either crushed or regurgitated; Arabic numbers in Roman face represent seeds that passed through the digestive tract of the corresponding bird. CL, *Celtis laevigata*; CA, *Convolvulus arvensis*; AM, *Arctium minus*; AT, *Abutilon theophrasti*; CF, *Cassia fasciculata*; RG, *Rhus glabra*; DC, *Desmodium canadense*; MP, *Malva parviflora*; RC, *Ratibida columnifera*; PV, *Prunella vulgaris*; LV, *Lepidium virginicum*; CHA, *Chenopodium album*; AP, *Amaranthus palmeri*. Species of birds used are as follows: goose, *Anser albifrons*; duck, *Anas platyrhynchos*; quail, *Coturnix coturnix*; killdeer, *Charadrius vociferus*; lesser yellowlegs, *Totanus flavipes*; least sandpiper, *Erolia minutilla*; pigeon, *Columba livia*; dove, *Zenaida asiatica*; green jay, *Cyanocorax yncas*; raven, *Corvus cryptoleucus*; mockingbird, *Mimus polyglottos*; starling, *Sturnus vulgaris*.

		CL	CA	AM	AT	CF	RG	DC	MP	RC	PV	LV	CHA	AP
Seed	Wt (mg)	104	18	10	11	9	7	5	2	0.6	0.8	0.3	0.7	0.3
	Length (mm)	6	4	5	4	4	3	3	2	2.5	2	1.5	1.2	0.9
Goose (2)		0	19	2	2		26		7					4
Duck (5)		24	5	0	0	0	27	0	28	0			5	12
Quail (5)		26	24	0	0	7	33	3	34	0	3	5	10	3
Killdeer (5)		*160*	*144*	*8*	*77*	*24*	*340*	*12*	*152*	2	16	15	6	15
Lesser yellowlegs (3)			*6*			*6*	*7*		*8*		*3*	8	8	12
Least sandpiper (5)							*216*		*123*		5			4
Pigeon (5)		*0*	*0*	*0*	*0*	*0*	*0*	*0*	24		3	6	0	14
Dove (5)			*0*	*0*	*0*	*0*	*0*	*0*	7	0		3	4	4
Green jay (3)			13			14	18		25	0	15			10
Raven (3)		17	8		8	12	14	12	12					
Mockingbird (3)		1	2		2	2	2				2			2
Starling (5)		2	10	15	5	15	15	15	15	3	8	6		5

only a few hours, may play a significant role in the movement of disseminules from upland to aquatic sites. Transfer of resistant seeds from one bird to another, that is, from a "commuter species" to a "transoceanic express" might reasonably be assumed to occur anywhere shorebirds mingle in mixed flocks during spring and autumn migration. We have observed birds reingest seeds cast up by regurgitation.

The third objection—that migratory birds empty the digestive tract before extended flight—may be significant, but at present there is little information either to support or to counter this theory. White-crowned sparrows and several other granivorous birds apparently empty the digestive tract before migration (*12*). However, food normally passes through these birds within 2 to 4 hours. As yet, it is not known whether shorebirds, particularly those that do not regurgitate pellets, are unable to voluntarily empty the gizzard.

VERNON W. PROCTOR
Department of Biology, Texas Technological College, Lubbock

References and Notes

1. R. W. Cruden, *Evolution* **20**, 517 (1966).
2. H. N. Ridley, *The Dispersal of Plants Throughout the World* (Reeve, Ashford, Kent, England, 1930), pp. 335–514.
3. "Long-distance" here means 1600 km or more (*4*). Since 64 to 80 km/hr is a reasonable approximation for the flight speed of most birds, seed retention intervals of 20 to 30 hours or longer would be needed to complete such flights.
4. S. Carlquist, *Island Life* (Natural History Press, New York, 1965), pp. 14–30; S. Carlquist, *Bull. Torrey Bot. Club* **94**, 129 (1967).
5. V. L. deVlaming and V. W. Proctor, *Amer. J. Bot.* **55**, 20 (1968).
6. Shorebirds were confined in compartments 40 by 60 by 50 cm. All other birds were in wire-mesh cages approximately twice this size, except for the geese which were in still larger cages. All birds were able to move about freely during the course of a retention trial. Separate trials were conducted for each seed species, and at least 24 hours elapsed between successive runs with the same birds. Food, water, and grit were available to birds before and throughout all experiments.
7. V. W. Proctor, C. R. Malone, V. L. deVlaming, *Ecology* **48**, 672 (1967).
8. All disseminules are here referred to as seeds, though by strict definition many were fruits. Fleshy or dry outer coverings, for example in *Celtis, Rhus, Desmodium,* and *Malva,* were removed before the seeds were presented to the birds. Viability of recovered seeds was determined either by germination or the use of tetrazolium (*5*).
9. C. R. Malone, *Wilson Bull.* **78**, 227 (1966); P. A. Stewart, *ibid.* **79**, 337 (1967); V. L. deVlaming, *ibid.*, p. 449.
10. Most shorebirds will regurgitate in 1 to 3 hours if given a gelatin capsule containing small glass beads. Gizzard contents can be sampled in this manner without killing the birds.
11. G. C. Munroe, *Birds of Hawaii* (Tuttle, Rutland, Vt., 1960) p. 58; F. A. Pitelka, *Condor* **61**, 233 (1959).
12. M. L. Morton, *Condor* **69**, 491 (1967).

27 February 1968

DNA (Cell Number) and Protein in Neonatal Brain: Alteration by Maternal Dietary Protein Restriction

Abstract. *Female rats were maintained on 8 or 27 percent protein diet by a pair-feeding schedule for 1 month before mating and throughout gestation. The brains of newborn rats from females on the 8 percent protein diet contained significantly less DNA and protein compared to the progeny of the females on the 27 percent diet. The data on DNA indicate that there are fewer cells; the protein content per cell was also lower. If, at birth, the brain cells are predominantly neurons, and their number becomes final at that time, then such dietary restriction may result in some permanent brain-neuron deficiency. This quantitative alteration in number as well as the qualitative one (protein per cell) may constitute a basis for the frequently reported impaired behavior of the offspring from protein-deprived mothers.*

The effects of malnutrition on development have been extensively studied. For brain, such studies were concerned mainly with the effects on weight or size (*1, 2*), which, however, depend on factors (such as lipids, water content) that do not reflect the number of brain cells. Winick and Noble (*3*) and Dickerson *et al.* (*4*) investigated the effect of malnutrition after birth on the DNA content of the brain. If the malnutrition occurred from birth to weaning, the animals (rats, pigs) exhibited a permanent brain DNA deficiency. The influence of malnutrition on learning behavior of rats has also been studied (*5, 6*). Many investigators have implied that protein deprivation before and after birth results in mental impairment in children (for reviews see *7*).

For the understanding of this influence of malnutrition on behavior, the study of changes in the number of brain cells is of interest. Whereas, in the rat the number of glial cells and the total number of brain cells increases for some time after birth (*8, 9*), the number of neurons does not increase (*8, 10, 11*), with the possible exception of short-axoned neurons (*11*). Thus, we studied the effect of maternal malnutrition before and during gestation, on the amount of brain DNA (brain cell number) in newborn animals.

Our report is a continuation of previous studies (*12, 13*) of factors influencing the amount of DNA in the brain, which reflects the number of brain cells because the DNA content of a diploid cell of a given species is constant; our eventual purpose is the elucidation of the relation between alterations in brain cell number and behavior.

We used albino rats derived from the Sprague-Dawley strain; these rats have been bred in our laboratory for at least ten generations; the females were virgin, 3 months old, and weighed 200 to 260 g. The animals were maintained (i) on powdered diets containing either 8 percent or 27 percent protein (*14*) by a pair-feeding schedule (intake 16 g/day); or (ii) another group was maintained on pelleted diet (*15*) as desired (16 g/day). The protein was casein. Both protein diets contained the same amounts of fats (10 percent) and salts (4 percent). In addition, the 8 percent protein diet contained 78 percent starch, and the 27 percent protein diet contained 59 percent starch. To both diets, 2.2 percent of Vitamin Diet Fortification Mixture in

Table 1. The effect of restriction of maternal dietary protein on weight and content of brain of newborns. Diet A, full pellet; B, full diet, containing 27 percent protein; C, restricted, containing 8 percent protein.

Diet	Number of animals: Mothers	Number of animals: Offspring	Offspring weights (g): Body	Offspring weights (g): Brain*	Brain content of offspring*: DNA (μg)	Brain content of offspring*: Protein (mg)
A	5	41	5.7 ± 0.4	0.159 ± 0.071	544 ± 20	
B	4	32	6.38 ± .4	.181 ± .014	546 ± 22	9.29 ± 0.43
C	4	31	4.46 ± .22	.139 ± .081	491 ± 29	7.45 ± .57
Decrease† (%)						
			30	23	10	19.8
Probability						
			$P<.001$	$P<.001$	$P<.001$	$P<.001$

* Cerebral hemispheres, without cerebellum and olfactory lobes. † Difference between 27 percent and 8 percent protein groups.