Wilson Bull., 98(4), 1986, pp. 526–534

TIMING AND LOCATION OF SPRING SPERM RELEASE IN NORTHERN THRUSHES

W. B. QUAY[1]

ABSTRACT.—Cloacal lavages were taken from 166 individuals, representing 4 species of North American thrushes (*Catharus fuscescens, C. ustulatus, C. minimus, Hylocichla mustelina*) at 3 sites during spring migration and the beginning of the breeding season. Sperm morphology was similar in the 3 species showing sperm, and in second-year (SY) and after-hatching-year (AHY) males. Cloacal sperm were not evident in Wood Thrushes and Veeries south of their nesting ranges, but were found in Swainson's Thrushes at sites 800 and 230 km south of their nesting range. Sperm numbers in the lavages were not correlated with time-of-day, size of cloacal protuberance, wing chord length, or age class. *Received 10 Oct. 1985, accepted 21 Mar. 1986.*

Five closely related American thrushes nest at higher northern latitudes: the Wood Thrush (*Hylocichla mustelina*), Veery (*Catharus fuscescens*), Hermit Thrush (*C. guttata*), Swainson's Thrush (*C. ustulatus*), and Gray-cheeked Thrush (*C. minimus*). Ecological associations and behavioral traits of these species have been studied and compared extensively (Wallace 1939; Bent 1949; Dilger 1956a, b, c, d; Annan 1962; Cochran et al. 1967; Hicks 1967; Noon 1981). Relatively few aspects, however, of their reproductive biology have been described (Weaver 1939; Dilger 1956a, e; Brackbill 1958; Annan 1963; Longcore and Jones 1969). Published information on thrush sperm is limited apparently to that of Retzius (1909), who reported on morphology in European taxa, and McFarlane (1963), who examined sperm from 3 genera and 7 species of turdids, but provided no further specifications or details.

This report presents comparative data on the timing and geographic locations of spring sperm release in Wood Thrushes, Veeries, Swainson's Thrushes, and Gray-cheeked Thrushes based upon cloacal lavages (Quay 1984) of 166 individuals taken at 3 sites. Important findings include: (1) Sperm are released by some male Swainson's Thrushes prior to arrival at, and south of, the geographic nesting range of the species. (2) There are probable species differences in the timing and geographic location of first sperm release. (3) Timing of sperm release varies from year to year, probably in relation to timing of spring migration and associated environmental and physiological factors.

[1] Bio-Research Laboratory, 2003 Ida St., Napa, California 94558.

METHODS

Study sites and times.—Collection of data and cloacal lavage specimens was at 3 sites (Table 1) that differed by being considerably south, slightly south of the nesting range, or well within the nesting range of the species studied. All species were lavaged at each of the sites, but the nesting ranges of only 2 of the species (Wood Thrush at Foley and Long Point, Veery at Long Point) encompassed one or both of the more northern sites.

The first site was a residential yard at the northeast end of the city of Galveston, Galveston County, Texas (29°19′N, 94°48′W), 1.6 km NW of the Gulf of Mexico. Birds were mist netted there at least several days per week throughout most of 1982, but spring migrant thrushes occurred during a limited period (Table 1). The second site was a farm 5 km NNW of Foley, Lincoln County, Missouri (39°08′N, 90°46′W), on the west bluffs of the Mississippi River Valley. Here diverse habitats were sampled with mist nets during the springs of 1983, 1984, and 1985. The third site was the "Old Cut Banding Station" of Long Point Bird Observatory (LPBO), within the base of peninsular Long Point, Ontario (42°34′N, 80°25′W). The site is within a major stopover area for migrating passerines (McCracken et al. 1981).

Species, sex, and age characterization.—All of the 166 thrushes contributing to this study were handled and lavaged by me. Thrushes in hand were readily identified to species, but sexing and ageing were frequently uncertain. A relatively large cloacal protuberance was taken to be the most reliable male criterion, and a distinct brood (incubation) patch was the most distinctive female criterion. Swainson's Thrushes were sexed by wing chord (Sheppard and Klimkiewicz 1976), but in rare cases when this was contradicted by cloacal protuberance or brood patch, the latter criteria were given priority. Spotted or streaked wing coverts constituted the sole criterion of second-year (SY) birds (Veery, Swainson's and Gray-cheeked thrushes) (U.S.D.I. 1977), although absence of such marks was not taken as a reliable indicator of older (ASY, after-second-year) age or "adulthood" (Payne 1961). Feather wear contributed additionally as an age criterion (Bond 1963).

Cloacal lavage specimens.—Cloacal lavages were taken within an hour of capture and just prior to banding and release (cf. Quay 1984; 1985a, b). On most occasions 2 lavages were made from each bird, the first without avoidable tactile stimulation and the second immediately following 20 gentle finger strokes bilaterally in the cloacal-vent region. The purpose of this was to try to ascertain whether cloacal sperm numbers and characteristics would be different in artificially stimulated emissions. Disposable plastic pipette tips (Cat. No. OME 1-100, Orthomedics, Inc., P.O. Box 247, Riverside, Connecticut 06878), fitted with rubber medicine dropper bulbs, were used to wash in and out of the cloaca aliquots of distilled or deionized water (salt crystals from alternatively tried saline solutions obscured sperm counts and caused artifacts). Such lavage aliquots were deposited on a clean 1 × 3 inch glass slide in sufficient volume to fill an elliptical area 40 × 20 mm.

The following improvements or modifications in previously reported techniques (Quay 1984, 1985a, b) were employed: (1) Slides ("Superfrost®," precleaned microscope slides, 1 mm thick, Cat. No. 12-550-12, Fisher Scientific Co., 711 Forbes Ave., Pittsburgh, Pennsylvania 15219) had one end frosted on one side to accommodate pencil labeling. (2) An ellipse, 40 × 20 mm inside dimensions, was marked on each slide using a cut cardboard or plastic guide and a red water-resistant felt pen, to retain a standard lavage volume on the slide. (3) A small (2 to 3 μl) drop of concentrated formalin was placed at the center of the elliptical area of each slide just before the lavage was added, both to fix the sperm and other lavage contents and to minimize the occurrence of artifacts during changes in tonicity and during drying. (4) Lavage pipette aliquot volumes of water of about 1.2 to 1.5 ml were employed. Generally 3 of these were combined per slide to fill the premarked elliptical area

TABLE 1

SITES, DATES, AND SPERM CONTENTS OF CLOACAL LAVAGES

Site and year			Dates (number with sperm/total number lavaged)			
			Wood Thrush	Veery	Swainson's Thrush	Gray-cheeked Thrush
Galveston, Texas		1982	27 Apr.–6 May (0/4)	25 Apr.–5 May (0/8)	22 Apr.–7 May (0/13)	18–28 Apr. (0/12)
Foley, Missouri		1983	7 May (0/1)		1 May (0/2)	2 May (0/1)
		1984	2–10 May (2/2)	7–11 May (0/3)	2–14 May (2/39)	2–14 May (0/21)
		1985	6–15 May (4/4)[a]	28 Apr. (0/1)	25 Apr.–1 June (0/9)	28 Apr.–11 May (0/4)[a]
Long Point, Ontario		1985	18 May (1/2)	17–24 May (3/11)[a]	17–24 May (6/27)[b]	19–23 May (0/2)
Totals						
Females				0/1	0/1	
Males	SY[c]				3/5	0/1
	AHY[d]		6/7	1/2	4/44	0/5
Unknowns	SY[c]			1/4	0/2	
	AHY[d]		1/6	1/16	1/38	0/34
All groups			7/13	3/23	8/90	0/40

[a] Includes one within-period recapture (e.g., one bird represented twice).
[b] Includes two within-period recaptures.
[c] SY = bird in second calendar year (year following hatching).
[d] AHY = bird in an after-hatching year (age otherwise unknown).

(total volume = 4.0–4.5 ml). After lavage of each bird, the pipette tip used was discarded and its bulb removed and thoroughly rinsed. Ordinarily neither the lavage water nor the lavage itself entered the bulb; however, avoidance of cross-contamination of slides by sperm from other birds or lavages is essential. Therefore, extreme care was taken to keep the slides, both before and after lavages, away from potential spattering during pipetting and by the birds themselves. Lavage slides (specimens) were labeled immediately, air-dried, and stored in dust-proof plastic slide boxes.

Quantitative methods.—Evaluation of the sperm content of the nonstained and noncovered cloacal lavages was done with phase contrast microscopy. The sperm head, or remaining portion closest to the head, constituted the point upon which sperm counts were based. When there were <500 sperm/slide, all sperm in the lavage area were counted; when there were between 500 and 50,000 sperm/slide, sperm were counted within 100 microscope field areas (0.079692 mm^2/field) at arbitrary intervals across and down the lavage area in a grid pattern; when there were >50,000 sperm/slide, they were counted within 50 such fields at arbitrary intervals. Total sperm/slide thus were counted (<500) or estimated (>500); estimations used the formula: sperm counted × πab/number of fields × 0.079692, where a and b are the semiaxes (usually 20 and 10 mm) of the elliptical lavage area on the slide.

RESULTS AND DISCUSSION

Thrush sperm in dried cloacal lavages were easily recognized on the basis of size, morphology, and optical properties. Cloacal sperm of the 3 species that released sperm were remarkably similar, at least at the level of phase contrast light microscopy (Fig. 1).

Wood Thrush.—None of the spring Wood Thrushes netted and lavaged at Galveston showed cloacal sperm, even though this locality is only about 150 km S and SW of the nearest limits of the species' breeding range (Oberholser 1974) on the Texas mainland. At the 2 sites within the nesting range, large fractions of Wood Thrushes lavaged in May had cloacal sperm (Table 1). Numbers of sperm per first lavage slide ranged from 1.6×10^3 to 196.0×10^3 without clear evidence of correlations with time-of-day, relative development of the cloacal protuberance (CP), or wing chord (Table 2). In 4 of 7 of the Wood Thrushes that released sperm, the post-massage lavage gave more sperm than the first lavage; 3 of these were the birds that gave the smallest numbers in the first lavage (Table 2).

Veery.—At Galveston and Foley, both south of the Veery's nesting range, none of 12 Veeries showed sperm. At Long Point, within the southern limits of the nesting range, 3 out of 11 individuals lavaged had sperm. One of these was an SY bird (spotted wing coverts) (Tables 1 and 2).

Swainson's Thrush.—This was the only species that released sperm south of the limits of its nesting range. Although sperm release was absent at Galveston, it occurred in 2 birds at Foley and in 6 at Long Point (Table 1). The latter 2 sites are 800 and 230 km S, respectively, of the limits of the nesting ranges. Sperm release at Foley was seen only in 1984, possibly because of smaller sample sizes in 1983 and 1985. The difference also

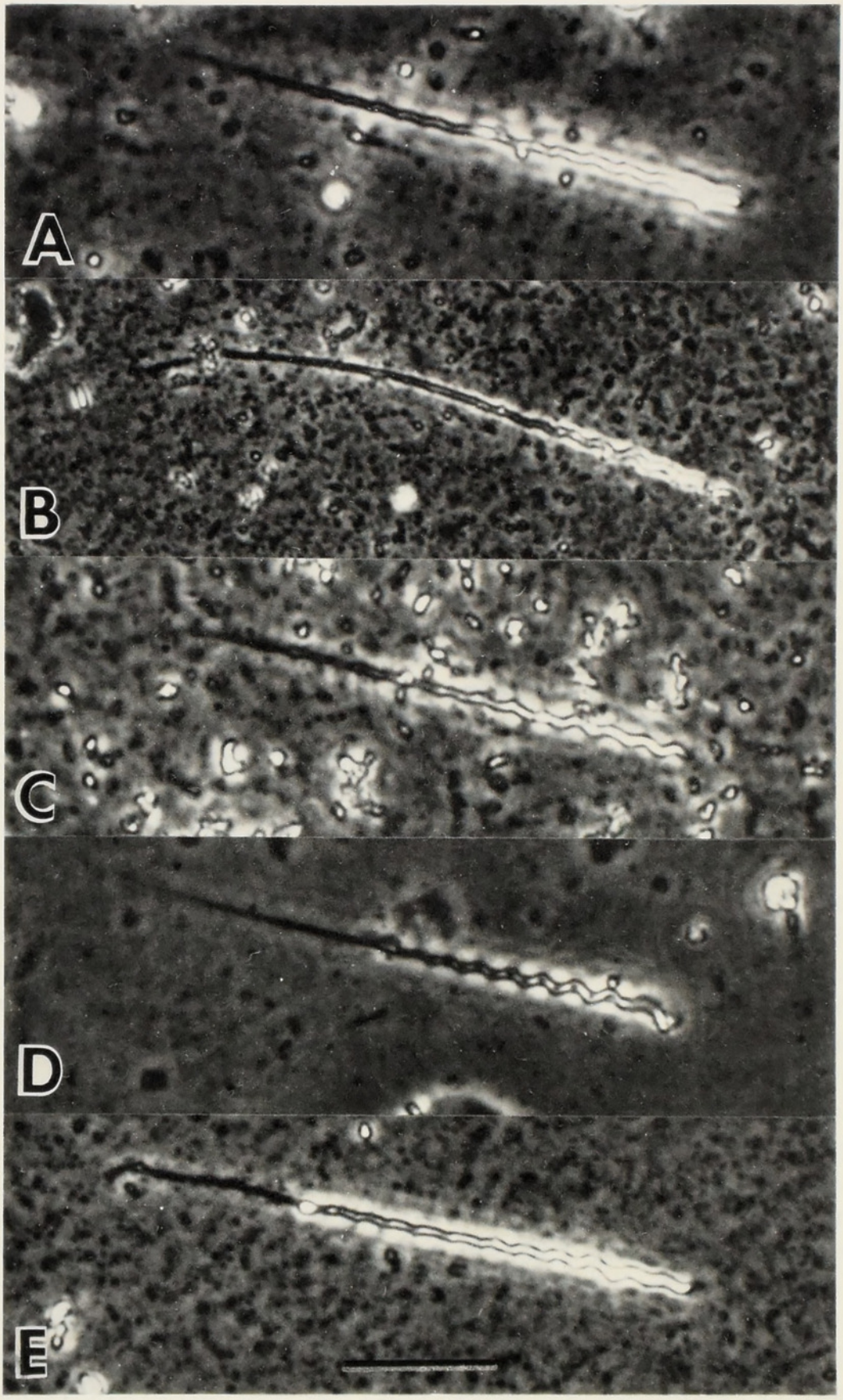

FIG. 1. Nonstained spermatozoa in cloacal lavages of thrushes, photographed with phase contrast microscopy. The relatively long, glistening, and spiraled heads are at the right, and

may have been influenced by the relatively early migration of Swainson's Thrushes in 1985, both at Foley and Long Point.

Maximum and mean cloacal sperm numbers were less in Swainson's than in Wood Thrushes (Table 2). This is more likely to be due to the representation of earlier phases of sperm release in the still migrating Swainson's Thrushes than in the largely on-territory Wood Thrushes, rather than to a true species difference in sperm numbers. Comprehensive quantitative cloacal sperm data from other free-living passerines have shown a characteristic increase in cloacal sperm numbers up to the third or peak phase of sperm release. This peak phase just precedes general occurrence of cloacal sperm in females (inseminated) of the particular population (Quay, unpubl. data). The present, more limited results from thrushes do indicate the efficacy and desirability of cloacal lavage samplings for comparing aspects of reproductive timing activity and potential in populations and species of thrushes. No relationships are evident between cloacal sperm numbers and time-of-day, relative size of the cloacal protuberance, wing chord length, or age (with vs without wing-covert spotting) for either species (Table 2).

Gray-cheeked Thrush.—None of the Gray-cheeked Thrushes lavaged at the 3 study sites had cloacal sperm (Table 1). As the distance between the most northern site and the southern limit of the nesting range of the Gray-cheeked Thrush is greater than the distance between the Swainson's Thrush's southernmost site with sperm release and its southern nesting limit, no conclusions can be drawn about possible differences between these species.

Age differences.—In Veeries and Swainson's Thrushes similar numbers of cloacal lavage sperm were released by SY and AHY birds (Table 2). Morphologically, as well as numerically, normal cloacal sperm were the same in the two age classes of birds (Fig. 1).

Biological meaning of cloacal sperm.—Results from cloacal lavages of free-living birds have indicated that reproductively active male passerines release sperm into the cloaca spontaneously and continuously (Quay 1984,

---

←

the tapered, dark tails extend to the left. (A) Male Wood Thrush at 06:14 CST, 15 May 1985 (6th Wood Thrush from Foley in Table 2). (B) Male Veery at 12:36 EST, 24 May 1985 (3rd Veery from LPBO in Table 2). (C) SY (spotted wing coverts) Veery at 07:48 EST, 19 May 1985 (1st Veery from LPBO in Table 2). (D) Male Swainson's Thrush at 08:00 CST, 14 May 1984 (2nd Swainson's Thrush from Foley in Table 2). (E) SY (spotted wing coverts; absent to trace cloacal protuberance) Swainson's Thrush at 10:13 EST, 20 May 1985 (5th Swainson's Thrush from LPBO in Table 2). All at the same magnification; the bar scale is 20 μm long.

TABLE 2

NUMBER OF SPERM PER LAVAGE SLIDE AND OTHER CHARACTERISTICS OF THRUSHES RELEASING SPERM

Species site	May date	Year	Time[a]	CP[b]	Wing chord (mm)	Wing covert spots[c]	Sperm per lavage slide	
							First slide	Postmassage
Wood Thrush								
Foley	2	84	08:00	1	107	0	1620	3630
	6[d]	85	07:46	0–1	102	0	147,000	58,800
	7[d]	85	17:50	2	102	0	196,000	12,200
	10	84	06:00	2	—	0	10,100	148,000
	15	85	06:14	4	105	0	8870	11,200
	15	85	07:48	4	106	0	92,400	21,900
LPBO	18	85	07:32	—	106	0	162,000	188,000
Mean							88.3×10^3	66.4×10^3
Veery								
LPBO	19	85	07:48	—	95	+	28,100	17,500
	19	85	09:05	—	98	0	2190	1440
	24	85	12:36	1	102	0	35,300	37,800
Mean							21.9×10^3	18.9×10^3
Swainson's Thrush								
Foley	12	84	06:00	0	—	0	0	493
	14	84	08:00	2	—	0	13,100	13,000
LPBO	19	85	09:07	1–2	96	0	8090	284
	19	85	09:59	4	99	0	5240	2040
	19	85	10:04	0–1	100	+	2	340
	20	85	09:56	2	99	+	64,300	18,000
	20	85	10:13	0–1	100	+	6620	20,100
	22[e]	85	09:10	1	95	0	568	3500
Mean							12.2×10^3	7.2×10^3

[a] Central (Foley, Missouri) or Eastern (Long Point Bird Observatory, Ontario) standard time.
[b] CP = relative size of cloacal protuberance on a scale of 0 to 5.
[c] 0 = absent; + = present.
[d] The same bird; lavaged and banded 6 May, recaptured and lavaged 7 May.
[e] This bird was lavaged and banded 4 days earlier, at which time it was not releasing sperm.

1985a, b). This interpretation has been confirmed by recent studies with captive passerines lavaged at 3- or 6-h intervals (Quay, unpubl. data). As a number of nonpasserine groups of birds do not show this behavior, it can be concluded that spontaneous and continuous sperm release need not indicate proximate copulatory or ejaculatory activity. This is consistent with the finding in the present study that migratory and nonpaired (by field study) male Veeries and Swainson's Thrushes were releasing sperm relatively early, in relation to the well known trend of the later

arrival of females of the same species (Weaver 1939, Dilger 1956a, Annan 1962, Bond 1963). The possible competitive and adaptive advantages of early sperm release by male thrushes remain to be determined. Nevertheless, my data from a number of different passerines indicate that early sperm release per se may not be immediately or directly important for fertile inseminations. Its importance appears to be in appropriately timed build up and maturation of seminal emission and contents, leading to the most propitious timing, numbers, and characteristics of seminal sperm for effective mating.

ACKNOWLEDGMENTS

I thank C. Quay for aid and understanding at all sites and through all phases of this study, W. and V. Knox for their hospitality and help at Foley, and M. McNicholl and others for hospitality and encouragement at Long Point.

LITERATURE CITED

Annan, O. 1962. Sequence of migration, by sex, age, and species, of thrushes of the genus *Hylocichla,* through Chicago. Bird-Banding 33:130–137.

———. 1963. Experiments on photoperiodic regulation of the testis cycle in two species of the thrush genus *Hylocichla.* Auk 80:166–174.

Bent, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull. 196.

Bond, G. M. 1963. Geographic variation in the thrush *Hylocichla ustulata.* Proc. U.S. Natl. Mus. 114:373–387.

Brackbill, H. 1958. Nesting behavior of the Wood Thrush. Wilson Bull. 70:70–89.

Cochran, W. W., G. G. Montgomery, and R. R. Graber. 1967. Migrating flights of *Hylocichla* thrushes in spring: a radiotelemetry study. Living Bird 6:213–225.

Dilger, W. C. 1956a. Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla.* Auk 73:313–353.

———. 1956b. Relationships of the thrush genera *Catharus* and *Hylocichla.* Syst. Zool. 5:174–182.

———. 1956c. Adaptive modifications and ecological isolating mechanisms in the thrush genera *Catharus* and *Hylocichla.* Wilson Bull. 68:171–179.

———. 1956d. Hylocichlid thrushes in captivity, with notes on their behaviour. Avicult. Mag. 62:183–189.

———. 1956e. Nest-building movements performed by a juvenile Olive-backed Thrush. Wilson Bull. 68:157.

Hicks, D. L. 1967. Adipose tissue composition and cell size in fall migratory thrushes [Turdidae]. Condor 69:387–399.

Longcore, J. R. and R. E. Jones. 1969. Reproductive success of the Wood Thrush in a Delaware woodlot. Wilson Bull. 81:396–406.

McCracken, J. D., M. S. W. Bradstreet, and G. L. Holroyd. 1981. Breeding birds of Long Point, Lake Erie. Canadian Wildlife Service, Ottawa, Canada.

McFarlane, R. W. 1963. The taxonomic significance of avian sperm. Proc. Int. Ornithol. Congr. 13:91–102.

Noon, B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51:105–124.

OBERHOLSER, H. C. 1974. The bird life of Texas. Vol. 2. Univ. Texas Press, Austin, Texas.

PAYNE, R. B. 1961. Age variation and time of migration in Swainson's and Gray-cheeked thrushes. Wilson Bull. 73:384–386.

QUAY, W. B. 1984. Cloacal lavage of sperm: a technique for evaluation of reproductive activity. North Am. Bird Bander 9(2):2–7.

———. 1985a. Cloacal sperm in spring migrants: occurrence and interpretation. Condor 87:273–280.

———. 1985b. Sperm release in migrating wood-warblers (Parulinae) nesting at higher latitudes. Wilson Bull. 97:283–295.

RETZIUS, G. 1909. Die Spermien der Vögel. Biol. Untersuch., New Ser. 14:89–126.

SHEPPARD, J. M. AND M. K. KLIMKIEWICZ. 1976. An update to Wood's Bird Bander's Guide. North Am. Bird Bander 1:25–27.

U.S.D.I. 1977. North American bird banding manual. Vol. II. U.S.D.I., U.S. Fish and Wildlife Service and Dept. Fisheries and Environment, Canadian Wildlife Service, Washington, D.C.

WALLACE, G. J. 1939. Bicknell's Thrush, its taxonomy, distribution, and life history. Proc. Boston Soc. Nat. Hist. 41:211–402.

WEAVER, F. G. 1939. Studies in the life history of the Wood Thrush. Bird-Banding 10: 16–23.

COLOR PLATE

The Frontispiece painting has been made possible by an endowment established by George Miksch Sutton. The painting is by James Coe.