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CLOACAL SPERM IN SPRING MIGRANTS: OCCURRENCE AND INTERPRETATION

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ABSTRACT.—Cloacal sperm were studied microscopically in cloacal lavages from 448 birds representing 70 migratory species, from Galveston, Texas, and Foley, Missouri. Representatives of 20 of these species sampled in the spring had cloacal sperm; at least 38 of the 39 individuals with sperm were males. A conservative interpretation of cloacal sperm in male migrants is that they represent spontaneous discharge from the ductus deferens or its glomus seminale, specifically in individuals that are ready for breeding. Although most of the migrants with cloacal sperm were not far from the known nesting range of the species, others were 30 to 900 km south of the southern limits of the known breeding range (Nashville Warbler [*Vermivora ruficapilla*], Rose-breasted Grosbeak [*Pheucticus ludovicianus*] and Painted Bunting [*Passerina ciris*]). There appear to be functionally significant differences among species of passerine birds in the timing of sperm emission and the physiological readiness for breeding; these processes apparently start in some species during spring migration.

This study is based chiefly upon my systematic collection and analysis of cloacal lavages (washes) from feral birds. The initial purpose of the lavage technique and its application during banding and field studies was to ascertain the feasibility of developing rapid, noninvasive, and repeatable methods for identifying the sex and physiological state of individual birds in the course of field studies and under natural conditions. My first notable finding from the use of this technique was that spermatozoa (sperm) can be found in the cloaca of reproductively active individuals of either sex and particularly in a number of passerines (Quay 1984a, b). This led to the present study, which had the goals of: (1) determining the occurrence of cloacal sperm in male spring migrants, (2) comparing species in these occurrences, (3) comparing results from two localities (Galveston, Texas, and Foley, Missouri) representing two latitudes in the central zone through the United States, and (4) making a start in determining the biological meaning of sperm in the cloacas of male migrants. A general review of some of this work has appeared in an abstract (Quay 1984b).

STUDY AREAS AND METHODS

I captured birds by mist nets, banded them and gave them cloacal lavages. During 1982, netting was done in the back and side yards of my residence at the NE end of the town of Galveston, Galveston County, Texas. Nets were in operation 6 and 14–31 March, 1–4, 14–21, and 25–30 April, and 1–13, 22, 26, 30 and 31 May, generally from before dawn to after sunset, and with breaks in the morning and afternoon. During 1983, the study area was a farm with mixed habitats on the bluffs on the W side of the Mississippi River, 5 km (airline) NNW of the town of Foley, Lincoln County, Missouri. Here, up to 16 nets were operated continuously from early in the day 30 April through early in the day 7 May 1983 (total = 98 net-days). Nets were inspected at approximately hourly intervals during the day and less frequently at night.

At both localities, I personally captured and processed all birds. After capture, birds were placed in individual light-weight, brown paper bags until processed about 5–20 min later. The procedural steps are noted here for two reasons: (1) they provide the basis for determinations of sex, age-class, and possible correlates of occurrences of cloacal sperm, and (2) they may possibly be related to presence or absence of cloacal sperm in some individuals or species through physical handling. Therefore, to facilitate the obtaining and interpreting of results of subsequent studies, all of the methods that I used are noted. These were: (1) weighing with a Mettler Type P-120 top-loading balance to the nearest 0.1 g; (2) measurement of wing chord and tail lengths; (3) determination of sex and age-class insofar as possible; (4) recording, where relevant, external characteristics such as the relative development of the cloacal protuberance of males, the size and degree of edema of the incubation/brood patch, and skull pneumatization; (5) banding; and (6) the taking of cloacal lavages. Procedures (2) through (5) above followed those of the "North American Bird Banding Manual vol. II (Bird Banding Techniques)" (Bird Banding Offices of the United States and Canada 1977). Determination of sex and age-class was based additionally upon critical and selective use of other published sources (Wood and Beimborn 1981, Oberholser 1974).

Cloacal lavages were taken by a procedure that has been described and evaluated elsewhere (Quay 1984a). One to six serial lavages were obtained from each bird and deposited on clean microscope slides. The latter were then air-dried under a 60–100 watt tungsten filament lamp and stored in slide boxes. I fixed and stained the lavage slides several weeks to nearly two years later, with equivalent satisfactory results. For higher power microscopy and photomicrography after staining, many of the slides were covered with a resin (Permount™) in xylene and a #1 thickness coverglass. I have discovered, however, that even in non-stained and non-covered slides, spermatozoa can be identified, counted, and photographed with phase-contrast microscopy using a Leitz Laborlux 12 compound binocular microscope.

The distinctive and relatively consistent morphology of avian spermatozoa enabled their identification even in the presence of diverse other kinds of cells and materials often occurring in cloacal contents. I scanned slides rapidly at a magnification of 100 × (10 × ocular, EF 10/0.25 PHACO 1 objective), but did all critical and quantitative studies at 400 × magnification (10 × ocular, EF 40/0.65 PHACO 2 objective). I estimated the total number of sperm per lavage (slide specimen) from counts of sperm in 100–300 microscope fields along multiple transects of the dried lavage area on the slide. The area of each field was 0.1590 mm^2. I determined the total area of each lavage either by planimetry of an enlarged outline tracing (camera lucida), or by the formula πab, when the lavage area on the slide approximated an ellipse. Therefore, the total number of sperm on a slide = sperm counted (πab)/ number of fields (0.1590). The arbitrary inclusion of a particular spermatozoon within a microscopic field for counting depended upon the occurrence within the field of half or more of the acrosomal portion. This relatively small but distinctive part was highly refractile and easily visible in both stained and nonstained slides. Fecal debris and the collection of sperm into balls sometimes posed difficulties. Even in those circumstances, however, sperm acrosomal regions could be counted using phase contrast microscopy.

I measured the lengths of sperm tails on camera lucida tracings. The latter were made from slides stained with Basic Fuchsin and viewed with phase-contrast optics at 400 ×, with a final magnification in the tracings of 600 ×. Calibration was done with a stage micrometer slide, and measurements were made with a precision opisometer (Minerva, Switzerland).

RESULTS

Sperm were identified easily in the cloacal lavage slides (Fig. 1). Many had evidence of structural modification, possibly owing in part to the actions of variable tonicities of the lavage solutions and of temperature and drying. The most frequent sign was swelling and occasional disruption of the head and mid-piece (e.g., Fig. 1, D–H).

Individuals of migratory species having cloacal sperm (Table 1) were of the greatest interest. These represented three categories. The first consisted of those species that were within their known breeding range, and for which ecological and behavioral observations suggested that the individuals with cloacal sperm may have been near their definitive breeding/nesting sites. I observed territorial and/or other prenesting behaviors in these species near the places where individuals with cloacal sperm were obtained concurrently. This category was represented by: Whip-poor-will, Eastern Bluebird, American Robin, Kentucky Warbler, Common Yellowthroat, Yellow-breasted Chat, Summer Tanager, Rufous-sided Towhee, Field Sparrow, Common Grackle, Bronzed Cowbird, and Northern (Baltimore) Oriole. It is possible that of these species, some of the individuals with cloacal sperm may have been still distant from their ultimate destinations or territories when they were captured and lavaged.

The second category contained species that were captured within their known breeding range, but ecological and behavioral observations indicated that the individuals with cloacal sperm were not near typical breeding or nesting areas. This category was represented by: Red-winged Blackbirds at Galveston, and Indigo Buntings at Foley. Red-winged Blackbirds at the Galveston study site occurred only as small groups of adult males from 17 March to 1 August. The earliest occurrence of cloacal sperm (4 April) in any of the birds was substantially earlier than the recognized start of the breeding season, mid-April, in Texas (Oberholser 1974). All Red-winged Blackbirds with cloacal sperm at Foley had already established territories with appropriate nesting habitat. Male Indigo Buntings lavaged at Foley (2–7 May) had cloacal sperm, but their behavior, and the dates, suggested that, with rare exception, they were in transit (Table 2).

The third category was that of individuals with cloacal sperm while considerably south, or outside, of their species' known breeding

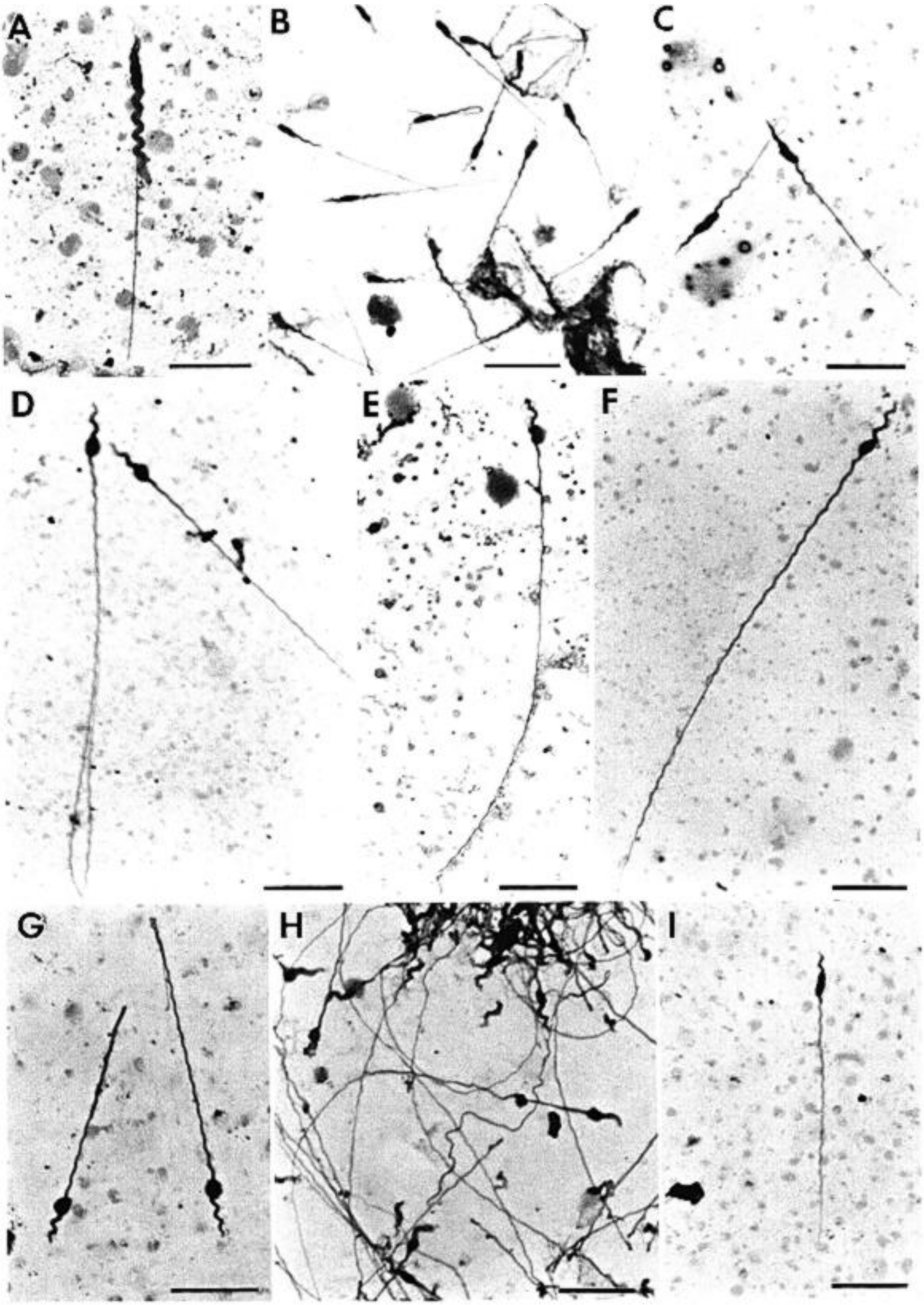

FIGURE 1. Photomicrographs of passerine spermatozoa in cloacal lavage slides stained with Basic Fuchsin. Bar length in the lower right corners of each panel equals 20 μm in the particular specimen. (A) Male Red-eyed Vireo, Foley, MO; 2 May, 11:20. (B) Male Gray Catbird, Foley, MO; 4 May, 06:00. (C) Brown Thrasher, Foley, MO; 3 May, 15:00. (D) Male Nashville Warbler, Foley, MO; 6 May, 06:30. (E) Male Kentucky Warbler, Foley, MO; 7 May, 08:00. (F) First-year male Red-winged Blackbird, Foley, MO; 5 May, 06:00. (G) Male Northern (Baltimore) Oriole, Foley, MO; 4 May, 09:00. (H) Uncertain sex Painted Bunting, Galveston, TX; 6 May, 07:29. (I) Male Yellow-breasted Chat, Foley, MO; 3 May, 16:30.

TABLE 1. Spring migrant species with sperm in cloacal lavages.

Species[a]	Site[b]	Birds: With sperm[c]	Birds: Total exam'd	Dates
Whip-poor-will (*Caprimulgus vociferus*)	F[d]	1m	1m 3f	05/01–02[e]–06
Eastern Bluebird (*Sialia sialis*)	F[d]	2m	2m 2f	05/02[e]–05
American Robin (*Turdus migratorius*)	F[d]	1m	1m	05/05[e]
Gray Catbird (*Dumetella carolinensis*)	G	0	25u	04/17–30
	F[d]	2m	3m	(05/02–04)[e]
Brown Thrasher (*Toxostoma rufum*)	F[d]	2m	3m 1f 1u	(05/01–04)[e]–07
Red-eyed Vireo (*Vireo olivaceus*)	G	0	17u	03/28–05/07
	F	1m	1m	05/02[e]
Nashville Warbler (*Vermivora ruficapilla*)	F	1m	2m	05/02, 06[e]
Kentucky Warbler (*Oporornis formosus*)	G	0	1m 7f	04/15–05/02
	F[d]	1m	2m 1f	05/04–07[e]
Common Yellowthroat (*Geothlypis trichas*)	G[d]	0	6m 4f	04/14–05/09
	F[d]	1m	2m	05/03,[e] 06
Yellow-breasted Chat (*Icteria virens*)	G	0	3u	04/26–28
	F[d]	1m	1m	05/03[e]
Summer Tanager (*Piranga rubra*)	G	0	10m 10f	03/30–05/05
	F[d]	1m	1m 1f	05/04[e]
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	G	1m	4m 4f	04/22–05/08[e]–11
	F[d]	1m	2m 1f	05/02, 05[e]
Indigo Bunting (*Passerina cyanea*)	G	0	23m 12f	03/30–05/06
	F[d]	5m	5m 2f	05/02[e]–07[e]
Painted Bunting (*Passerina ciris*)	G	1u	2m 5f 1u	04/15–05/06[e]–09
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	F[d]	1m	1m	05/04[e]
Field Sparrow (*Spizella pusilla*)	F[d]	1m	2m	05/04,[e] 06
Red-winged Blackbird (*Agelaius phoeniceus*)	G[d]	4m	10m	03/17(04/04–05/30)[e]
	F[d]	6m	7m 2f	05/03–05)[e]
Common Grackle (*Quiscalus quiscula*)	G[d]	2m	4m 1f	03/30–(05/22)[e]
Bronzed Cowbird (*Molothrus aeneus*)	G[d]	2m	2m 1f	04/17[e]–05/11[e]
Northern (Baltimore) Oriole (*Icterus galbula*)	G[d]	0	4m	04/15–05/08
	F[d]	1m	1m	05/04[e]

[a] Sequence and names follow AOU (1983).
[b] G = Galveston, Texas; F = Foley, Missouri.
[c] m = males, f = females, u = sex uncertain.
[d] These sites within known breeding/nesting range of the species.
[e] Dates (or date range) for capture of birds with cloacal sperm, within dates (or date range) for all captures with lavages.

range. They were a Nashville Warbler at Foley, Rose-breasted Grosbeak and Painted Bunting at Galveston. The characteristics and circumstances of these individuals warrant particular attention:

Nashville Warbler.—One of two males netted and lavaged at Foley had abundant cloacal sperm. The first of the two lavages taken contained 25,500 and the second 33,800. Total cloacal, or releasable, sperm were probably well in excess of the observed total of 59,300. This bird, captured and lavaged at 06:30 on 6 May, was still over 300 km away from the nearest known breeding area of the species (Pitelka 1940, Griscom et al. 1979, AOU 1983).

Rose-breasted Grosbeak.—This is a common migrant at Galveston, but I know of no breeding records for it there or elsewhere in Texas (Hall et al. 1959, Oberholser 1974). Its known breeding range, in northern deciduous forests, includes Foley, Missouri, but stops 900 km north of Galveston (AOU 1983). One of the five males lavaged at Galveston, and one of the two lavaged at Foley, had cloacal sperm. Sperm densities and numbers in the serial lavages from these birds decreased precipitously, and the totals were significantly different (Table 3). Each of the two males having cloacal sperm was closely attended by a female. At Galveston, the attending female remained near the male while he was in the net and rejoined him immediately after he was released. At Foley, the bird with cloacal sperm had the plumage of a first spring male and was captured with a female lacking sperm. Other males (four at Galveston and one at Foley) lacking cloacal sperm did not have apparent attending females in the vicinity.

Painted Bunting.—One of the five birds in female-type plumage and lavaged at Galveston (at 07:29 on 6 May) had cloacal sperm. Three birds in full male plumage and similarly processed at the same site lacked cloacal sperm. The individual with cloacal sperm was at the upper end of the size range for females. Since male Painted Buntings in their first breeding plumage often closely resemble adult females (Oberholser 1974), it is wise to consider the sex of the sperm-bearing individual as uncertain. Cloacal sperm were present in all six serial lavages, but the number per lavage declined after lavage number 2 (Table 4). Painted Bun-

TABLE 2. Numbers of cloacal sperm in male Indigo Buntings at Foley, Missouri.

Date	Time	Lavages: Number of slides	Lavages: Total sperm $\times 10^{-3}$	Lavages: $\bar{x}$ Sperm $\times 10^{-3}$ per slide
7 May	08:00	2	452	226
6 May	08:00	3	122	40.7
7 May	08:00	2	5.37	2.69
2 May	19:30	1	5.35	5.35
2 May	19:30	2	0.664	0.332

tings are known only as "common migrants" on Galveston Island, as noted by earlier observers (Hall et al. 1959) and as supported by my observations from 1977 to 1983. Breeding records are available, however, for the near coastal mainland of Texas (Oberholser 1974). Suitable habitat for breeding and nesting Painted Buntings on the Texas mainland occurs within 30–50 km of the Galveston site where the bird with cloacal sperm was captured.

Of the 70 migratory species (448 individuals) lavaged at either or both Galveston and Foley for this study, 20 (39 individuals) had cloacal sperm (Table 1). Birds representing half (10) of these sperm-bearing species were captured and lavaged at both localities. Eight of these lavaged at both localities had cloacal sperm only at Foley. The comparison of results from Galveston and Foley (Table 1) for these species is important in relation to possible interpretations of preterritorial sperm in migrants at Foley in comparison with what was found in migrants at Galveston. Therefore, I report both absences and occurrences of cloacal sperm in samples from these species at both localities (Table 1).

Species whose cloacal lavages failed to show cloacal sperm in migrants at any locality are listed below. This is done to provide a helpful database for further studies, in which cloacal sperm will probably eventually be found in some of these species but not in others, for reasons which are obscure at the present time. Sequence and names follow AOU (1983). Names, collection site (G = Galveston, F = Foley), number lavaged by sex (m = male, f = female, u = sex uncertain), and date(s) are given:

White-winged Dove (*Zenaida asiatica*) G: 1f, 4u, 03/31–05/31. Yellow-billed Cuckoo (*Coccyzus americanus*) G: 1u, 04/26. Chuck-will's-widow (*Caprimulgus carolinensis*) G: 1f, 04/17; F: 1f, 05/06. Yellow-bellied Sapsucker (*Sphyrapicus varius*) G: 3f, 03/23–29. Eastern Wood-Pewee (*Contopus virens*) G: 5u, 04/17–05/06. Yellow-bellied Flycatcher (*Empidonax flaviventris*) G: 1u, 05/02. Acadian Flycatcher (*E. virescens*) G: 2u, 04/26. Eastern Phoebe (*Sayornis phoebe*) G: 1u, 05/07. Great Crested Flycatcher (*Myiarchus crinitus*) F: 1f, 2u, 05/04–07. Eastern Kingbird (*Tyrannus tyrannus*) G: 1m, 03/27; F: 2u, 05/01–05. Purple Martin (*Progne subis*) G: 2m, 1f, 03/28–04/20. Tree Swallow (*Tachycineta bicolor*) G: 1f, 03/27. Blue-gray Gnatcatcher (*Polioptila caerulea*) G: 4u, 03/27–28. Veery (*Catharus fuscescens*) G: 8u, 04/25–05/08. Gray-cheeked Thrush (*C. minimus*) G: 12u, 04/18–28; F: 1u, 05/02. Swainson's Thrush (*C. ustulatus*) G: 14u, 04/22–05/07; F: 2u, 05/01. Wood Thrush (*Hylocichla mustelina*) G: 4u, 04/27–05/06; F: 1u, 05/07. White-eyed Vireo (*Vireo griseus*) G: 2u, 03/28, 04/04. Yellow-throated Vireo (*V. flavifrons*) G: 2u, 03/31–04/27. Blue-winged Warbler (*Vermivora pinus*) G: 1f, 04/21. Tennessee Warbler (*V. peregrina*) G: 9m, 9f, 04/19–05/01; F: 1m, 05/07. Northern Parula (*Parula americana*) G: 1m, 03/26. Yellow Warbler (*Dendroica petechia*) G: 1m, 1f, 04/21, 05/04. Chestnut-sided Warbler (*D. pensylvanica*) G: 2m, 04/26–27. Magnolia Warbler (*D. magnolia*) G: 4m, 05/07. Cape May Warbler (*D. tigrina*) G: 1m, 1f, 05/01, 13. Yellow-rumped (Myrtle) Warbler (*D. coronata*) G: 1f, 03/20; F: 12m, 9f, 2u, 05/01–07. Black-throated Green Warbler (*D. virens*) G: 1f, 05/11; F: 2m, 05/02, 04. Blackburnian Warbler (*D. fusca*) G: 1m, 04/28. Palm Warbler (*D. palmarum*) F: 4u, 05/01–02. Bay-breasted Warbler (*D. castanea*) G: 5m, 05/07–12. Blackpoll Warbler (*D. striata*) G: 2m, 05/04, 06. Black-and-white Warbler (*Mniotilta varia*) G: 5m, 3f, 03/26–04/27; F: 1f, 05/02. American Redstart (*Setophaga ruticilla*) G: 2m, 5f, 04/27–05/11; F: 1m, 05/07. Prothonotary Warbler (*Protonotaria citrea*) G: 6m, 4f, 03/28–05/01. Worm-eating Warbler (*Helmitheros vermivorus*) G: 3u, 03/28–04/30. Swainson's Warbler (*Limnothlypis swainsonii*) G: 1u, 04/14. Ovenbird (*Seiurus aurocapillus*) G: 10u, 04/22–05/08; F: 1m, 05/06. Northern Waterthrush (*S. noveboracensis*) G: 9u, 04/18–30. Louisiana Waterthrush (*S. motacilla*) G: 3u, 03/30–05/05. Mourning Warbler (*Oporornis philadelphia*) G: 1m, 05/07; 1f, 05/02.

TABLE 3. Densities (number/mm^2) and total numbers of sperm in serial lavage slides from two male Rose-breasted Grosbeaks. A. from Galveston, 16:34, 8 May 1982. B. from Foley, 06:45, 5 May 1983.

Individual	Slide #	Density	Total number
A	1	35.2	46,500
	2	3.58	6,420
	3	0.755	967
	4	0.377	570
	5	0.377	653
	6	0.566	811
	Total		55,900
B	1	0.189	273
	2	0.0419	59
	3	0.0000	0
	Total		332

TABLE 4. Densities (number/mm^2) and total numbers of sperm in serial cloacal lavage slides from a Painted Bunting (sex? #960-73283).

Slide #	Density	Total number
1	7.93	13,800
2	27.2	55,200
3	1.38	2,540
4	1.51	2,210
5	0.566	888
6	0.440	736
Total		75,374

Hooded Warbler (*Wilsonia citrina*) G: 2m, 4f, 03/21–04/27. Canada Warbler (*W. canadensis*) G: 1m, 04/26. Scarlet Tanager (*Piranga olivacea*) G: 4f, 05/03–09. Blue Grosbeak (*Guiraca caerulea*) G: 1m, 1f, 04/21, 05/07. Chipping Sparrow (*Spizella passerina*) F: 1m, 05/02. Swamp Sparrow (*Melospiza georgiana*) F: 1u, 05/03. White-throated Sparrow (*Zonotrichia albicollis*) F: 2m, 1f, 05/01–03. Brown-headed Cowbird (*Molothrus ater*) G: 1m, 1f, 03/31, 04/26; F: 2f, 05/01, 03. Orchard Oriole (*Icterus spurius*) G: 7m, 5f, 04/02–07.

DISCUSSION

This research is based on the premise that careful study of numbers, characteristics, timing, and associated circumstances of cloacal sperm will contribute better understanding of comparative avian reproductive biology. It is to be expected that sperm occur in the cloaca in association with reproductive activity. Even so, I know of no published investigations of the spontaneous occurrence of cloacal sperm in feral birds, outside of my own recent work (Quay 1984a, b). One can surmise that two assumptions above all have deterred ornithologists from considering study of cloacal sperm to be a possibly fruitful enterprise. First, there is the cloacal mixing of sperm with fecal debris, urinary concentrates, micro-organisms, and sloughed epithelial and leucocytic cells. Nevertheless, I have found in practice that these inclusions usually do not prevent either recognition of sperm, or their quantitative study (Quay 1984a). This is a consequence of careful technique combined with relative diluting out of other cloacal contents. The second likely assumption, which also is untrue, is that cloacal transit by sperm is necessarily brief and infrequent. A brief post-ejaculatory interval is not the only time of cloacal occurrence of sperm, especially in males.

Sexually active male birds of many species spontaneously drain sperm into the cloaca (Quay 1984a, b, and unpubl.). This phenomenon has been noted in domestic cockerels (*Gallus gallus var. domesticus*; de Reviers 1975). Its study, however, has been limited to mammalian subjects (Aronson 1949, Orbach 1961, Beach and Eaton 1969). Even here it is often empirically difficult to differentiate between "spontaneous" or nonstimulated ejaculation and intermittent or continuous drainage of sperm from the male tract. Quantification of sperm production in both birds and mammals has often depended upon outputs in frequently stimulated, or artificial, ejaculations. Lino et al. (1967), however, suggested that "counting the number of spermatozoa in the urine of unejaculated males may be a simple method of estimating DSP [daily sperm production] in a variety of animals." My results indicate that such a procedure is possible and worthy of evaluation in feral male birds. Nevertheless, the relative quantitative contributions of "spontaneous emission" to the exterior, disintegration, and/or phagocytosis within the male tract remain to be determined. It is usually assumed that the first of these is quantitatively the most important (Fernández-Collazo et al. 1971, de Reviers 1975).

A problem still exists in distinguishing *a posteriori* sperm released by "spontaneous emission" from those released through stimulated ejaculation. Two kinds of stimulated ejaculation are at issue: (1) ejaculation under natural conditions and associated with normal breeding activity, and (2) ejaculation induced by handling or other artificial stimuli. There is insufficient evidence, as yet, for supposing that the first of these two kinds of ejaculation was responsible for cloacal sperm in our preterritorial male migrants. Presumably, effective breeding and insemination did not occur during migration. The second kind of ejaculation also seems unlikely as the best explanation, on the basis of several kinds of evidence. Although stroking or massaging can lead to artificial induction of ejaculation in at least some species (Quinn and Burrows 1936; Wolfson 1952, 1960; see Gee and Temple 1978 for later references), four lines of evidence suggest that this is an infrequent or unlikely explanation for cloacal sperm in my lavaged migrant males: (1) Handling of male non-domesticated birds, and of birds not sexually imprinted on humans, inhibits the ejaculatory reflex and release of sperm and, instead, prompts defecation and urination (Lake 1978, Gee and Temple 1978). (2) My handling of the birds during processing and lavage was rapid, gentle, and minimal; there was, furthermore, no massaging or stroking. (3) In the instances where serial lavage samples were obtained from individual males showing cloacal sperm, the number of sperm was maximal or near maximal in the first, and sometimes the second, lavage and declined markedly in later ones, as in the Rose-breasted Grosbeaks (Table 3). If the lavage procedure had been inducing ejaculation or release of sperm, it might be supposed that later lavage samples would be more likely to contain greater numbers of sperm. (4) In a recent experimental study using several different feral passerine species, I tested the effect of gently massaging or "milking" the paracloacal region of males having a well developed cloacal protuberance here. Two cloacal lavages were taken before the massage and at least one following it. Maximal numbers of cloacal sperm usually occurred immediately after the paracloacal massage and these numbers generally greatly exceeded those which were ever obtained by simple lavage alone. Some of the individual passerine males tested showed cloacal sperm, but only after the paracloacal massage. Others showing cloacal sperm before paracloacal massage had relatively low numbers. Other kinds of procedures and circumstances were tested, and marked individual variations between birds were noted. For this reason, the presentation and analysis of this experimental study is best deferred, but the above observations from it tend to support the conclusion that cloacal lavage itself need not induce ejaculation or major release of sperm into the cloaca.

The most important observation from this study is that sperm release occurs in spring migrant males of some species while they are still distant from their nesting territories. This extra- or pre-territorial release of normal sperm (Fig. 1) into the cloaca is a far more cogent criterion of physiological readiness for breeding than is testicular size or presence of sperm in testis or epididymis. Sperm taken from either the testis or epididymis have a much lower capacity to fertilize than do those from the ductus deferens (Munro 1938, Murton and Westwood 1977). A necessary functional maturation follows the structural maturation of the sperm.

Among the migrant species represented by the greatest numbers of males, species differences are suggested in the relative timing of sperm release into the cloaca. For example, sperm release occurred in a migrant male Rose-breasted Grosbeak while still far from the known breeding range, but not in any of the male Summer Tanagers (Table 1) although they were approaching more closely the known breeding range of the species. Study of such species differences, using large sample sizes, more times of sampling, and localities representing more latitudes and habitats will be desirable. The early or pre-territorial sperm release of some species is probably related to a reproductive optimization strategy, in the sense of Dunbar (1983). This habit may be adaptively most significant in the case of migrant species with relatively short nesting seasons in northern latitudes. It also seems likely, and worthy of testing, that early or pre-territorial sperm release may be linked with early laying in some species. The variable importance of, and some of the conditions giving advantage to, early laying of eggs have been reviewed by Rowley (1983). These would seem in many instances to be relevant as well in consideration of the possible biological correlates and importance of early sperm release in migrants.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. Am. Ornithol. Union, [Washington, DC].

ARONSON, L. R. 1949. Behavior resembling spontaneous emission in the domestic cat. J. Comp. Physiol. Psychol. 49:226–227.

BEACH, F. A., AND G. EATON. 1969. Androgenic control of spontaneous seminal emission in hamsters. Physiol. Behav. 4:155–156.

BIRD BANDING OFFICES OF THE UNITED STATES AND CANADA. 1977. North American Bird Banding Manual. Vol. II. Bird banding techniques. U.S. Fish and Wildlife Service, Dept. of the Interior, Washington, D.C.

DE REVIERS, M. 1975. Sperm transport and survival in male birds, p. 10–16. *In* E. S. E. Hafez and C. G. Thibault [eds.], The biology of spermatozoa. Transport, survival and fertilizing ability. S. Karger, Basel.

DUNBAR, R. I. M. 1983. Life history tactics and alternative strategies of reproduction, p. 423–433. *In* P. Bateson [ed.], Mate choice. Cambridge Univ. Press, Cambridge.

FERNÁNDEZ-COLLAZO, E., E. VIDELA, AND J. C. PEREYRA. 1971. Elimination of spermatozoa in the urine of isolated male rats. J. Reprod. Fertil. 27:145–147.

GEE, G. F., AND S. A. TEMPLE. 1978. Artificial insemination for breeding non-domestic birds. Symp. Zool. Soc. Lond. 43:51–72.

GRISCOM, L., A. SPRUNT, JR., AND E. M. REILLY, JR. 1979. The warblers of America. Doubleday & Co., Garden City, NY.

HALL, C. E., J. E. HILDEBRAND, R. T. BINHAMMER, AND O. HALL. 1959. The birds of Galveston Island. Texas J. Sci. 11:93–109.

LAKE, P. E. 1978. The principles and practice of semen collection and preservation in birds. Symp. Zool. Soc. Lond. 43:31–49.

LINO, B. F., A. W. H. BRADEN, AND K. E. TURNBULL. 1967. Fate of unejaculated spermatozoa. Nature (Lond.) 213:594–595.

MUNRO, S. S. 1938. Functional changes in fowl spermatozoa during their passage through the excurrent ducts of the male. J. Exp. Zool. 79:71–92.

MURTON, R. K., AND N. J. WESTWOOD. 1977. Avian breeding cycles. Clarendon Press, Oxford.

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

ORBACH, J. 1961. Spontaneous ejaculation in rat. Science (Wash. DC) 134:1072–1073.

PITELKA, F. A. 1940. Nashville Warbler breeding in northeastern Illinois. Auk 57:115–116.

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

QUAY, W. B. 1984b. Cloacal sperm in passerine birds: Comparative differences in vernal timing, cytodynamics, physiological correlates and endocrine-reproductive strategies. Am. Zool. 24:71A.

QUINN, J. P., AND W. H. BURROWS. 1936. Artificial insemination of fowls. J. Hered. 27:31–37.

ROWLEY, I. 1983. Re-mating in birds, p. 331–360. *In* P. Bateson [ed.], Mate choice. Cambridge Univ. Press, Cambridge.

WOLFSON, A. 1952. The cloacal protuberance—a means for determining breeding condition in live male passerines. Bird-Banding 23:159–165.

WOLFSON, A. 1960. The ejaculate and the nature of coition in some passerine birds. Ibis 102:124–125.

WOOD, M., AND D. BEIMBORN. 1981. A bird-bander's guide to determination of age and sex of selected species. 2nd. ed. Afton Press, Afton, MN.

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The Condor 87:280

RECENT PUBLICATIONS

Bird banding.—Elliott McClure. 1984. Boxwood Press. 341 p. Paper cover. $15.00 plus $1.00 for shipping. Source: Boxwood Press, 183 Ocean View Blvd., Pacific Grove, CA 93950. This is a manual on banding birds (and bats), a revised version of the author's 1966 work. It is based on his extensive experience, chiefly in southeast Asia, yet draws liberally on the literature of banding. After introductory material, it surveys *every* family of birds as to its idiosyncrasies for being caught and handled. A series of chapters then considers traps, snares, nets, banding nestlings, and miscellaneous equipment. Reflecting McClure's expertise about birds as carriers of zoonoses, another chapter gives instructions for collecting ectoparasites, preparing blood smears, and taking blood, thereby making more use of captured birds. A final, emphatic chapter explains how to keep records. The writing is clear and nontechnical, though less tightly organized than it might be. Details are illustrated with many drawings and photographs. Although the book does not purport to be a complete and comprehensive manual, it is so full of practical advice as to be valuable for novice and advanced banders alike. References, index.

Avian osteology.—B. Miles Gilbert, Larry D. Martin, and Howard G. Savage. 1981. Published by B. Miles Gilbert, Laramie, Wyoming. 252 p. Paper cover. $20.00. Source: Publications Secretary, Museum of Natural History, The University of Kansas, Lawrence, KS 66045; add $2.00 for postage and handling; Kansas residents add 3.5% sales tax. This is a manual for the identification of bird bones as found in archaeological sites, chiefly in North America. It deals with the skeletal elements that are most commonly collected, and therefore omits the skull, vertebrae, ribs, and most of the phalanges. Treatment for each bone includes a general description, illustrations for many species, and a table of measurements for many species. Several bones are also furnished with keys for identification to order or family. Taxonomic coverage is largely confined to non-passerines, the passerines being represented in almost every case by only four corvids. Since the photographs and soft pencil drawings of the bones are likely to be used first in identifying specimens, it is unfortunate that they have been variously enlarged or reduced. Thus, even on the same plate, homologous bones that are actually the same size are often shown at different sizes. Several full-page historic photographs of Native Americans show how bones and feathers were incorporated into their regalia but do not tell anything about the structures themselves. Although the book is aimed for archaeologists, it may prove useful to ornithologists confronted with the remains of avian prey from raptor nests. References.

The growth and development of birds.—Raymond J. O'Connor. 1984. John Wiley & Sons, Chichester and New York. 315 p. No price given. This book explores how and why birds grow as they do, i.e., not just what happens but also its adaptive meaning. Organized around the life history of a bird, it integrates current ideas and findings on physiology, ecology, and behavior. After a survey of the growth patterns among birds and their ecological significance, several chapters lead from nests and eggs through the development of the chick, feeding, imprinting, and parental care. A chapter on mortality of eggs and young is followed by those on instinct and learning, development of song, migration, and maturation. Tying together material from diverse fields, it provides a coherent picture of the ecological constraints on the breeding biology of different birds. Since this book impinges on virtually every aspect of ornithology, it is one of the most widely interesting works in the science to have appeared in a long time. Illustrations, references, index.

Current ornithology, Volume 2.—Edited by Richard F. Johnston. 1985. Plenum Press, New York. 364 p. $39.50. Following the pattern of its predecessor (noted in Condor 87:13), this volume contains nine advanced-level review articles on topics of current interest. Highly worth reading is the opening chapter by F. C. James and C. E. McCulloch on data analysis and the design of experiments in ornithology. The following, more specialized chapters are: The evolution of reversed sexual dimorphism in size (by H. C. Mueller and K. Meyer), Vocal "dialects" in Nuttall's White-crowned Sparrow (D. E. Kroodsma, M. C. Baker, L. F. Baptista, and L. Petrinovich), On the nature of genic variation in birds (G. F. Barrowclough, N. K. Johnson, and R. M. Zink), Ecomorphology (B. Leisler and H. Winkler), Problems in avian classification (R. J. Raikow), Syringeal structure and avian phonation (A. S. and S. L. L. Gaunt), Assessment of counting techniques (J. Verner), and Circadian organization of the avian annual cycle (A. H. Meier and A. C. Russo). The book has been well edited except for misspelling of two authors' names in the preface. Since this series uniquely occupies its niche in the community of ornithological literature, one hopes that it will continue. Illustrations, lists of references, indices.