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INSEMINATION OF TENNESSEE WARBLERS DURING SPRING MIGRATION[1]

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Abstract. Possible occurrence of insemination, and circumstances of sperm release and insemination, during spring migration were studied with the aid of cloacal lavages from 139 Tennessee Warblers (*Vermivora peregrina*) sampled and released at Galveston, Texas, Foley, Missouri, and Long Point, Ontario, 1982 to 1988. Twenty-five percent (13/52) of females at Foley had been inseminated recently and were members of a subgroup having greater wing and tail lengths. Crown color was not associated with sperm release or insemination. Males releasing sperm at Foley averaged greater in body weight and earlier in time of capture during the day. Number of males releasing sperm and number of sperm being released per male increased progressively during the migration period at Foley. Early and late females were not inseminated. Inseminated females occurred during the 8 days, 5 to 12 May, of transit by most conspecifics and of males releasing sperm. Circumstantial evidence suggests that nutritional and social factors influenced migrant insemination. It is unknown to what extent, if any, such inseminations contribute to fertilizations and eventual offspring on the northern nesting territories after migration.

Key words: Tennessee Warbler; Vermivora peregrina; *abnormal sperm; cloacal lavage; crown color; insemination; mating preference; migration; sexual differences; spermatozoa.*

INTRODUCTION

Continuous spontaneous release into the cloaca of large numbers (often 10^4 to 10^6 per sample) of spermatozoa (sperm) characterizes reproductively active males of many species of passerine (Order Passeriformes) birds (Quay 1984, 1985a, 1987a). This mode of sperm release was discovered, and can be analyzed, through means of cloacal lavage and ancillary methods (Quay 1984, 1986a, 1986c, 1987a). Results from study of both free-living and aviary-held passerine males show that this continuous spontaneous passerine mode of sperm release differs from the usually considered or assumed avian modes of sperm release (Quay 1984, 1986a, 1986c, 1987a). The latter can be assigned to two general categories: (1) stimulated and spontaneous (nonstimulated) ejaculations, and (2) passive drainage of excess or overage stored sperm. Further investigation of the passerine mode of sperm release is important for the evaluation of fertility of individuals, and of the ways by which functionally significant transfer of sperm occurs and is controlled or modified in natural populations.

North American wood-warblers (Parulinae) present additional reasons for closer study of sperm release. Males of some of their species nesting at higher latitudes release sperm during spring migration, and while still far south (>640 to 1,490 km) of the limits of their geographic nesting ranges (Quay 1985b). The hypothesis offered was that such apparently precocious sperm release may represent an evolutionary adaptation for more rapid onset of reproduction in regions with short summers and associated ecological limitations. It can be asked as well whether this sperm release during migration is merely a token of early preparedness for breeding on the nesting grounds, or whether it may represent something more, such as capabilities for, and conceivably occurrences of, inseminations enroute.

The Tennessee Warbler (*Vermivora peregrina*) is one of the four species of wood-warblers shown to have males releasing sperm south of the nesting range. Further studies, reported here, demonstrate insemination of female comigrant Tennessee Warblers and describe the distinctive geographic, temporal, and physical characteristics of spring migrant male releasers of sperm, and of their female recipients.

METHODS

STUDY LOCATIONS AND TIMES

Collection of data and cloacal lavage samples from migrating Tennessee Warblers was done at

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three localities. Two of these, NE end of the city of Galveston, Galveston County, Texas (29°19'N, 94°48'W) and a farm about 5 km NNW from the town of Foley, Lincoln County, Missouri (39°08'N, 90°46'W), have been described previously (Quay 1985a, 1985b). The third was the "Old Cut" (Boulevard) banding station of Long Point Bird Observatory (LPBO), situated near the base of Long Point (42°32'N, 80°7'W), a peninsula extending into Lake Erie from its northern or Ontario, Canada, side (map and detailed description in McCracken et al. [1981]). The Galveston and Long Point localities figured in this study only 1 year each, 1982 and 1985 respectively, and served chiefly in comparisons with Foley, Missouri, concerning changes in Tennessee Warblers during their spring migration across the United States.

Investigations at Foley were annual for six consecutive springs from 1983 to 1988. Series of mist nets were in operation there in: 1983—30 April to 7 May, 1984—1 to 14 May, 1985—25 April to 16 May and 27 May to 1 June, 1986—3 April to 1 June, 1987—21 May to 8 June, and 1988—9 to 15 May. The dates in 1987 were relatively late in relation to the usual dates of passage by Tennessee Warblers and none were observed or caught. Therefore, 1987 does not appear in tabulations or other results. Netting at Galveston occurred at least several days per week through 1982, and migrant warblers were captured there from 20 March to 13 May, 1982. Research and associated netting at Long Point was limited to 17 to 24 May, 1985.

CAPTURE AND PROCESSING OF BIRDS

All birds were captured with mist nets and banded ("butt-end," closed, numbered metal bands; of Canadian Wildlife Service and U.S. Fish and Wildlife Service) by authorized persons. At Foley, nets were operated nearly continuously but for times or anticipations of inclement weather, usually at night. During daylight, nets were checked and birds removed generally at 30- to 60-min intervals. At night the intervals were longer. Estimated times of capture (to the half-hour) and net site number were usually noted for each bird. Number of nets in operation on any day at Foley was usually about the same through the migration period of transit by Tennessee Warblers. Tabulation of netting efforts at Foley, 1983–1986, has been provided (Quay 1987b). Netting efforts within each season were nearly constant from before dawn to after dark. Number of nets and particular net sites used varied in part from year to year, in relation to shifting objectives and environmental conditions. At first my emphasis was on sampling diverse habitats; later, especially in 1987 and 1988, it was on maximizing numbers of emberizids and concentrating upon the previously most productive sites and habitats. Therefore, unbiased year-to-year quantitative comparisons of captures of a particular species or subgroup may not be possible from my data as a whole.

Sexing of all captured birds was multifactorial and based upon standard plumage characteristics and wing and tail measurements (Raveling and Warner 1965, Sealy 1985, Pyle et al. 1987). Sealy (1985) has noted that "plumage characteristics remain the most effective way to sex Tennessee Warblers in spring because 98.6% accuracy was attained using this method" in Manitoba. Presumptive distinctions between age classes were subtle if present and usually could not be made with confidence.

Preliminary processing of birds consisted of weighing, measuring (wing chord, and at Galveston and Foley, tail length), taking notes on plumage, sexual/reproductive characteristics, and abnormalities and pathologies if superficially evident. Birds were then given cloacal lavages by methods described previously (Quay 1984, 1986b, 1986c, 1987a). From 1986 onward, four lavage slides were prepared from each bird. The first three were associated with minimal stimulation of the bird and served to washout cloacal sperm. The fourth or last lavage immediately followed a gently bilateral anterior-to-posterior stroking of the skin around the vent. The purpose of this was to possibly bring down some of the sperm that might be in the glomus seminale of males or in proximal regions of the reproductive tract of females. A small (0.02 to 0.04 ml) drop of concentrated formalin was placed by graduated syringe on each slide before the addition of lavage sample. This arrested microbial activity and fixed the sperm and other organic inclusions, thus minimizing potential artifactual modifications during tonicity changes and drying. Distilled water for lavages was used in pipette tips fitted with rubber medicine dropper bulbs and in aliquots of about 0.05 ml. The pipette tip was discarded and the bulb rinsed and dried after use with each bird. Contamination was prevented also by taking lavages while slides other than the

TABLE 1. Localities, years, and categories of specimens of Tennessee Warblers in this study.

Categories	Localities	Galveston, Texas	Foley, Missouri						LPBO, Ontario	Totals
	Years	1982	1983	1984	1985	1986	1988	Subtotal	1985	All
Captured:	Males	11	1	3	11	31	14	60	4	75
	Females	18	0	1	3	39	15	58	9	85
	Totals	29	1	4	14	70	29	118	13	160
Lavaged:	Males	9	1	3	11	27	14	56	4	69
	Females	9	0	1	3	33	15	52	9	70
	Totals	18	1	4	14	60	29	108	13	139
With cloacal sperm:	Males	0	0	2	1	10	11	24	2	26
	Females	0	0	0	0	8	5	13	0	13
	Totals	0	0	2	1	18	14	37	2	39
Percent with cloacal sperm:	Males	0	0	67	9	37	79	43	50	38
	Females	0	0	0	0	24	30	25	0	18
	Totals	0	0	50	7	30	48	34	15	28

intended ones were not exposed to possible accidental spatter from birds or pipettes. All birds were immediately released unharmed following these procedures.

QUANTITATIVE METHODS

Sperm numbers and characteristics were determined through the use of phase contrast microscopy, without staining or covering the dried lavage specimens on slides. These have remained unchanged in this form in dust-proof slide boxes for many years (1982–1988). Total numbers of sperm per bird were rounded to three places. Differential counts of normal and abnormal sperm in lavage slides from a 1988 sample of males and females used a precalibrated ocular scale for measurement of sperm length at 100×, and at 400× to check for smaller kinds of structural abnormality. Photomicrography utilized "Kodak Technical Pan Film 2415" (ASA usually set at 50) in a Leitz Laborlux 12 compound photomicroscope.

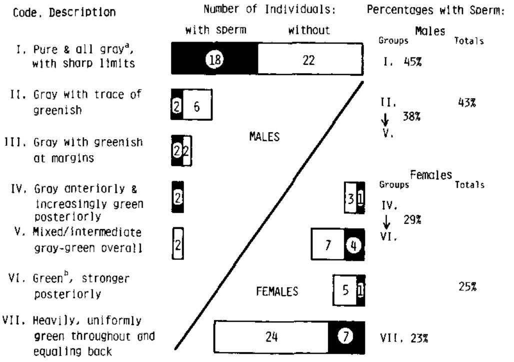

FIGURE 1. Crown colors and patterns in relation to sex and occurrence of cloacal sperm in spring Tennessee Warblers at Foley (all years, 1983–1988, combined). Seven crown color patterns are described and coded (I–VII). [a] "Gray" varied from light to darker tones, and sometimes had slightly blue tints, of "Color 86 Pale Neutral Gray" of Smithe (1975). [b] "Green" was generally near "Color 50, Yellowish Olive-green" of Smithe (1975).

Comparisons of results in the form of two samples (e.g., males vs. females, or with vs. without sperm) sometimes employed the Student-Fisher *t* and ANOVA, but more often had to depend upon nonparametric statistics, usually the Wilcoxon's two-sample test (Sokal and Rohlf 1969, p. 392–394). Data expressed as percentages were subjected to arcsine transformation prior to calculations, and results were evaluated by confidence limits (Sokal and Rohlf 1969, p. 386–387, 145–148, respectively). Possibilities of relationships between numbers of sperm and other characteristics or circumstances were studied by means of plots, ANOVA, and in selected cases, Model I regressions (Sokal and Rohlf 1969, p. 404–405, 431–432, 495–498). In the study of frequency distributions of measurements and their possible departure from a normal curve, the normal curve derivative was calculated and the observed distribution compared with this, utilizing Kolmogorov-Smirnov (Sokal and Rohlf 1969, p. 114, 573; Conover 1980) and chi-square tests for goodness of fit (Sokal and Rohlf 1969, p. 569; Beyer 1984, p. 296).

RESULTS

Numbers and categories of Tennessee Warblers studied are summarized in Table 1. Differences

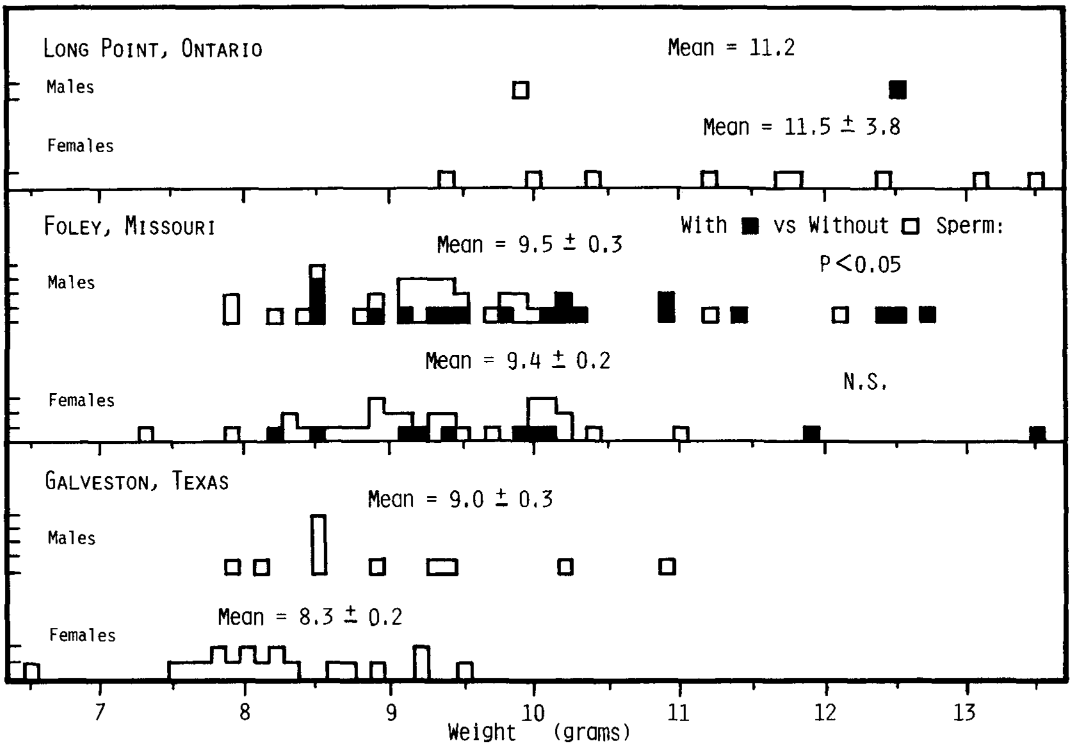

FIGURE 2. Body weights and occurrences of cloacal sperm in migrant Tennessee Warblers at the three localities. Numbers of individuals are given in Table 1. Increase in body weight was progressive latitudinally, and insemination occurred only in birds at mid-latitude (Mississippi Valley).

in numbers between years at Foley are most likely due chiefly to increased netting efforts and more selectively productive net sites in later years. Major attention in the present study is directed to the 24 males and 13 females at Foley that had cloacal sperm.

CHARACTERISTICS OF BIRDS WITH SPERM

Crown color. The two extremes (I and VII) of crown color typified 71% of males and 60% of females, respectively (Fig. 1). Individuals with intermediate crown color were not significantly different from typical members of their sex in the occurrence of cloacal sperm (Fig. 1). Thus there was no evidence of an assortative relationship between crown color or pattern and sperm release in males or insemination in females.

Body weight. As might be expected, body weights increased in both sexes at higher latitudes (Fig. 2). Although the three localities are probably not so aligned as to provide samples from the same major breeding Tennessee Warbler populations, they are still likely to be representative of the species' pattern of changes during the methodical transit from south to north across the United States. Females containing cloacal sperm were found only at Foley. A trend occurred of male sperm release and female insemination in the heaviest birds and their absence in the lightest ones (Fig. 2). In the male sample from Foley but not the female one, birds with sperm were significantly different statistically from those without, in body weight distribution ($P < 0.05$ two-tailed, Wilcoxon's two-sample test, Fig. 2).

Wing chord. Males with and without cloacal sperm did not differ significantly in wing chord length, but females did (Fig. 3). The frequency distributions of all male values, or of subgroups with and without sperm, resemble normal curves. Although comparable distributions of the females' values are suggestive of bimodality (Fig. 3), chi-square and Kolmogorov-Smirnov tests for goodness of fit failed to provide a basis for rejection of the null hypothesis regarding normal-

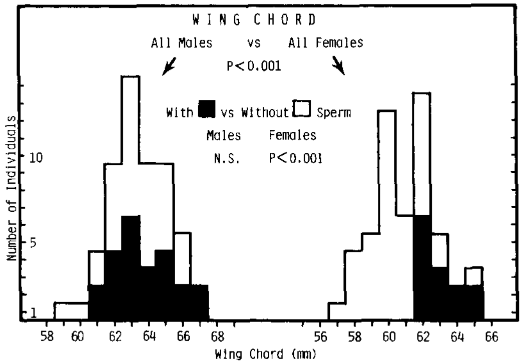

FIGURE 3. Frequency distributions of wing chord lengths in Tennessee Warbler males and females at Foley, and in their subgroups with and without cloacal sperm.

ity. Therefore, means ± their standard errors (and numbers of individuals) were noted: all males—63.46 ± 0.24 (54); all females—61.06 ± 0.27 (51) in mm. These means were significantly different (Fig. 3, Student-Fisher *t*), in confirmation of previous reports of this sexual difference in wing length (Raveling and Warner 1965, Oberholser 1974, Shepard and Klimkiewicz 1976, Sealy 1985, Pyle et al. 1987).

Tail length. In major respects differences in tail length related to sex and sperm occurrence paralleled those in wing chord length (Fig. 4). However, the observed frequency distribution of female tail lengths is significantly unlike the normal curve derivative ($P < 0.01$ by two-sided Kolmogorov-Smirnov test, and $P < 0.001$ by chi-square test for goodness of fit). Females with cloacal sperm occurred in the segment of the bimodal distribution representing greater tail lengths (Fig. 4), and females with and without sperm differed significantly in their tail length distributions ($P < 0.02$, two-tailed Wilcoxon's two-sample test). Tail length distributions were sexually significantly different ($P < 0.001$), but still overlapped.

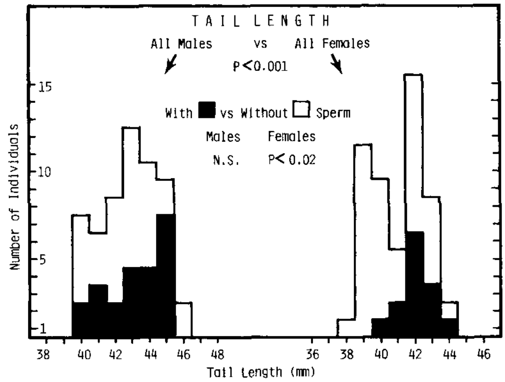

FIGURE 4. Frequency distributions of tail lengths in Tennessee Warbler males and females at Foley, and in their subgroups with and without cloacal sperm.

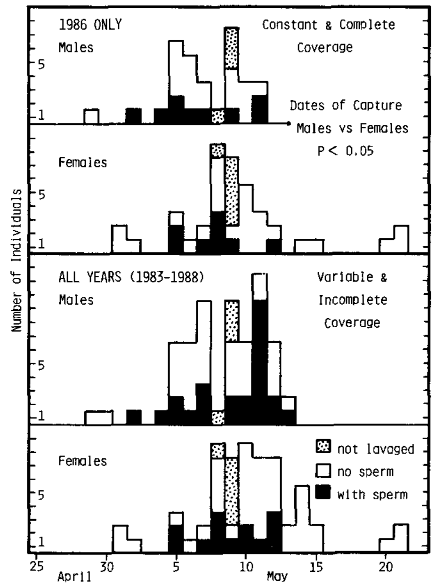

FIGURE 5. Frequency distributions of capture dates of Tennessee Warblers at Foley. In 1986 (upper two panels) netting activity and effort were essentially continuous and constant from 3 April to 1 June, and daily coverage was complete from before light to after dark. In other years (data added in lower panels = "all years") netting days probably did not include all spring days during which Tennessee Warblers were in the area.

CHRONOLOGY OF SPERM RELEASE AND INSEMINATION

Comparison of localities. At Galveston, on the coast of the Gulf of Mexico, neither sperm release nor signs of insemination were found in Tennessee Warblers during any part of the time of arrival and transit. But at Foley, near midcourse up the Mississippi Valley, 43% of the males were releasing sperm and 25% of the females had been inseminated recently (Table 1, Fig. 1). Then, farther north, at Long Point, although male sperm release was still occurring, none of the nine females sampled showed sperm; sample size here was too small to support firm conclusions. Although no cloacal lavage data are available from populations of Tennessee Warblers on their nesting grounds in mid- to northern Canada, it is

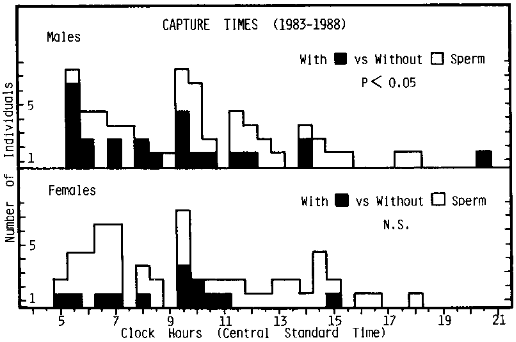

FIGURE 6. Frequency distributions of estimated capture times at Foley of Tennessee Warbler males and females with and without cloacal sperm.

TABLE 2. Total numbers[a] of sperm per bird in relation to sex and date.[b]

May dates	Males	Females
2	652 (86)	
4	932 (86)	
5	5,890 (86)	807 (86)
	208 (86)	4 (86)
6	3,390 (86)	
7	31,900 (84)	3 (86)
	3,610 (85)	
	1,350 (86)	
8		21,100 (86)
		1,320 (86)
		7 (86)
9	442 (86)	232 (86)
	64 (86)	
10	150 (88)	1,170 (88)
	77 (88)	114 (88)
11	16,900 (84)	
	409 (86)	
	9 (86)	
	54,600 (88)	33,100 (88)
	41,100 (88)	
	30,200 (88)	
	21,700 (88)	
	20,100 (88)	
	5 (88)	
12	102,000 (88)	22,600 (86)
	486 (88)	68,200 (88)
		11,400 (88)
13	6,160 (88)	

[a] For each bird all lavage slides' results were combined (no recaptured birds).

[b] All years combined; years in ( ).

assumed that male sperm release and insemination of females occur there. My Long Point locality is 150 km south of the southernmost site of "possible breeding evidence" and 370 km south of the southernmost site of "confirmed breeding evidence" for the species in Ontario (Cadman et al. 1987, Peck and James 1987).

Spring migration at Foley. Tennessee Warblers appeared to pass through Foley in the spring with little pause, and observationally, chiefly as brief waves. None of the 118 captured and banded there in the spring was ever recaptured there. Most of the birds were captured within a span of 8 days, 5 to 12 May, with a very few males being the earliest arrivals (29 to 30 April) and a few females comprising the late stragglers (15 to 21 May) (Fig. 5). Distributions of capture dates were significantly different between males and females ($P < 0.05$, Wilcoxon's test). However, birds with sperm occupied chiefly the middle dates of passage through Foley, with a tentative trend of increasing numbers of sperm-releasing males in later major waves (Fig. 5, third panel), and inseminated females closely coincided with and followed sperm-releasing males (Fig. 5).

Time of day. Males releasing sperm tended to be captured earlier in the day than those without sperm ($P < 0.05$, two-tailed Wilcoxon's two-sample test), and inseminated females were not distinctive in their times of capture (Fig. 6).

NUMBERS AND CHARACTERISTICS OF THE SPERM

Sperm numbers. Numbers of cloacal sperm varied greatly individually (Table 2), even though the lavage technique and volumes were standardized as well as possible. This variation in males was probably due to different phases and rates of sperm release being represented, and in females due to different seminal volumes being delivered and different lengths of time postinsemination. There was a tendency for greater sperm abundance on later dates, particularly in males, and paralleling greater relative numbers of males releasing sperm at this time (Fig. 5). However, the reality of such a trend on a year-to-year basis is uncertain, since representations by year in the data are slight and erratic (Table 2). Nevertheless, the maximum cloacal sperm number, 102,000 seen in a male on 12 May, is comparable to peak cloacal sperm numbers seen in locally nesting warblers of other species.

There was no apparent assortative relationship between number of cloacal sperm in either males or females and crown color and pattern (Table 3). It is yet interesting that for both sexes, both prime for the sex and intermediate crown colors

TABLE 3. Total numbers[a] of sperm per bird in relation to sex, year (1984–1988), and crown color (I–VII).[b]

			Crown color code			
I	II	III	IV	V	VI	VII
	Males					
31,900 (84)	442 (86)	5,890 (86)	409 (86)			
16,900 (84)	5 (88)	54,600 (88)	6,160 (88)			
3,610 (85)						
3,390 (86)						
1,350 (86)						
932 (86)						
652 (86)						
208 (86)						
64 (86)						
9 (86)				Females		
102,000 (88)						
41,100 (88)						22,600 (86)
30,200 (88)						21,100 (86)
21,700 (88)						1,320 (86)
20,100 (88)				68,200 (88)		807 (86)
486 (88)				11,400 (88)		232 (86)
150 (88)				1,170 (88)		4 (86)
77 (88)			3 (86)	114 (88)	7 (86)	33,100 (88)

[a] For each bird all lavage slides' results were combined (no recaptured birds).
[b] Key in Figure 1.

were represented by individuals with maximal or near maximal numbers of cloacal sperm. This is consistent with a lack of assortative relationship between crown color and relative numbers of individuals containing sperm (Fig. 1)

Sperm characteristics. Brief characterization here of the cloacal sperm of the male and female Tennessee Warblers has the limited purpose of contributing information useful in interpreting the meaning of cloacal sperm in these migrants. Tennessee Warbler sperm were relatively long and structurally of the general passerine type (Fig. 7), as described in other species by McFarlane (1963), Humphreys (1972), and Henley et al. (1978). Sperm balls (Quay 1986b) along with isolated sperm occurred in many of the lavages from Tennessee Warblers at Foley. In males, the lavages with sperm balls and near maximal numbers of sperm were similar to those of resident passerine breeders near the peak of their breeding activity.

DISCUSSION

INTERPRETATION OF CLOACAL SPERM IN FEMALES

Cloacal sperm in migrant female Tennessee Warblers corresponded structurally to recent (within about a day) inseminations rather than to washout voidings that can be expected several days or weeks after inseminations in resident passerines that I have studied by cloacal lavage. It is reasonable to postulate that in passerines as in domestic fowl (Kamar and Hafez 1975), immediately after insemination sperm are distributed rapidly throughout the oviduct and disappear from the lumen itself within about a day. I find that resident passerine females lavaged through the breeding and nesting season have a second appearance of postinsemination sperm in the cloaca. In this final voiding of the sperm, cloacal lavages show chiefly fragmented or disintegrating sperm along with depleted remains

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FIGURE 7. Photomicrographs at the same magnification of sperm in cloacal lavages taken 10 and 11 May 1988, from Tennessee Warblers at Foley, Missouri. A. Normal spermatozoan from a male (crown color code I). B. Near normal (tail tip at left folded and fused) spermatozoan from a female (crown color code V). C. Abnormal (slight to extreme) spermatozoa, examples of FFA (Fold-fusion anomaly), in a male (crown color code I). D. Edge of a small sperm ball from a female (crown color code VII); most of the sperm here have the FFA and/or have lost their heads; heads (glistening and refractile in phase contrast) of two apparently normal sperm are at the lower left and more are at the right. The scale bar = 50 μm.

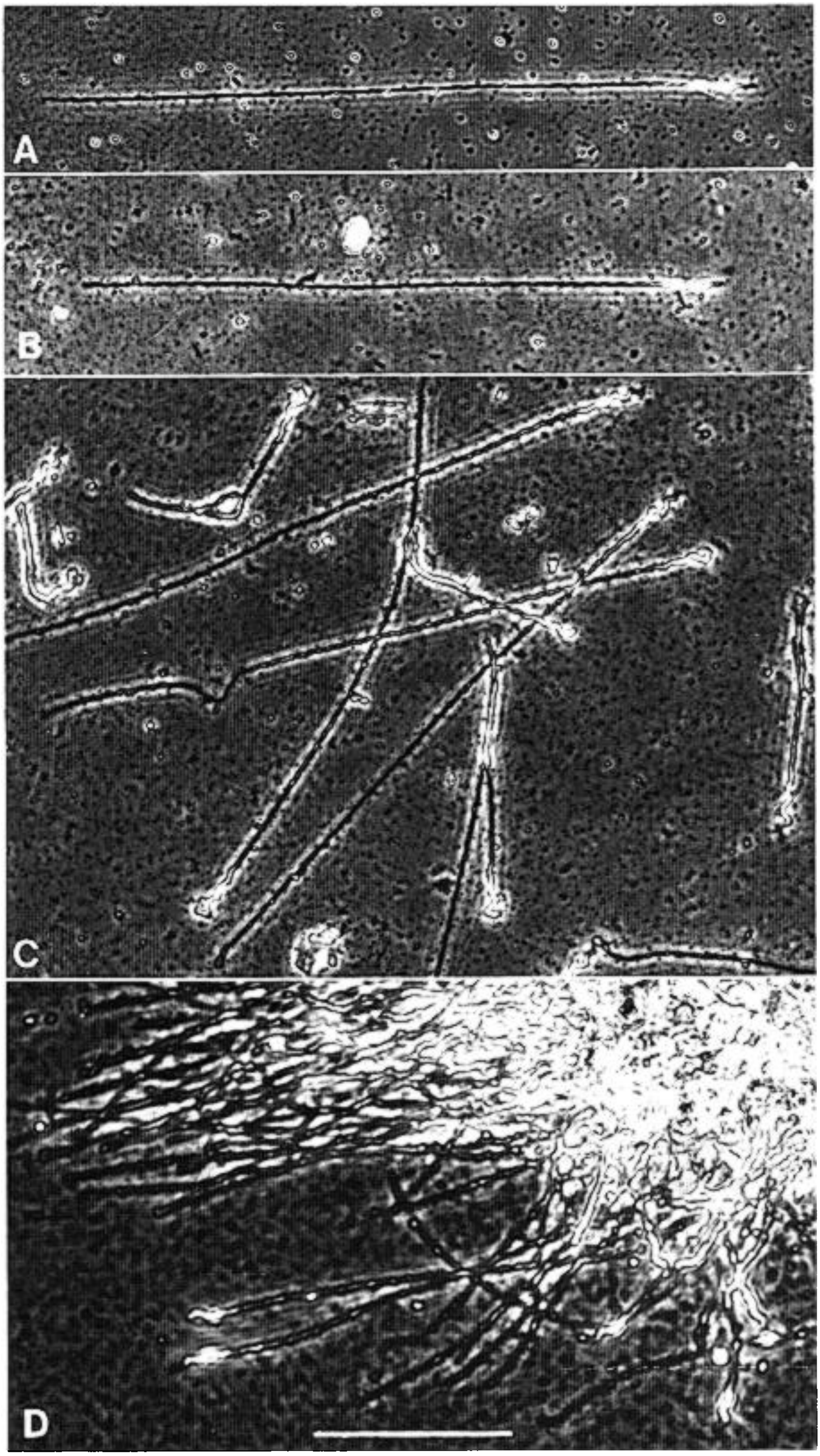
A
B
C
D

TABLE 4. Percentages of normal and abnormal sperm in cloacal lavages from male and female Tennessee Warblers at Foley, Missouri in 1988.[a]

		Abnormal			
	Normal	Short[b]	Headless	Structurally anomalous	Total abnormal
Males	72.58%	0.04%	0.41%	26.97%	27.42%
Females	54.14%	1.47%	1.62%	42.77%	45.86%
P[c]	<0.05	<0.02	ns	ns	<0.05

[a] Data are mean percentages (reconverted from arcsine transformations used in calculations, Sokal and Rohlf, 1969, p. 386–387) based upon samples of 10 males and 5 females lavaged 10 to 13 May 1988.

[b] Sperm total lengths <120 μm.

[c] P values (from Wilcoxon's two-sample test) related to probability that distributions of values from males and females are equivalent.

of sperm balls. In contrast to this picture, lavages taken from resident female passerines within a short time after insemination *always* show *some* normal sperm and often a few small sperm balls. But progressively soon after insemination, as lavage sperm and sperm balls diminish in numbers, presumably due to their prompt passage up the female reproductive tract, percentage of lavaged sperm that are abnormal increases. This is the pattern observed in the sperm-containing lavages from female Tennessee Warblers at Foley (Table 4). These residual cloacal sperm probably consist of the defective and less motile ones that have failed to ascend or be taken up the female tract. The increased percent among these of structurally anomalous sperm, such as those in Figure 7C, demonstrates a negative selective process at work here rather than a degenerative process in situ within the cloaca. This is based upon my observation that these same kinds of grossly anomalous sperm are found in testicular smears and are the results of defective early development within the testis rather than of any subsequent process. All of the sperm-containing female-derived lavages of Tennessee Warblers are qualitatively of this *early postinsemination type,* whether the total number of remaining cloacal sperm was large or small. The *late postinsemination type* of cloacal lavage picture, seen in females of various passerine species some days or weeks after insemination, was not found in any of the migrant female Tennessee Warblers.

Important questions remain, such as whether, and if so in what way(s), insemination during migration actually contributes to reproduction and to reproductive strategies by the species. It is conceivable that there may be other biological explanations than direct contributions to reproduction. Hypothetically there might be some physiological and/or behavioral advantages to the individual in a kind of inseminatory practice run before the nesting territory is reached. On the other hand it remains hypothetically possible also, and experimentally testable, that the inseminated female migrant stores this early sperm in her tract and that it may have the potential for contributing to fertilizations some time later. We cannot therefore conclude that these inseminations necessarily have the opportunity to contribute directly to fertilization, without additional kinds of evidence which are not presently available.

FACTORS IN THE SPERM RELEASE AND INSEMINATION OF MIGRANTS

Results of this study do provide some clues, however, concerning probable factors in the occurrence of sperm release and insemination in spring migrants of this species. Such clues derive from the comparative differences in circumstances and characteristics of birds with and without sperm.

Level of nutrition. Level of nutrition as expressed by body weight appeared to be significantly related to sperm release and insemination (Fig. 2). On the Texas coast there was no cloacal sperm in either sex, and body weights were low, sometimes to the point of affected birds showing behavioral disabilities (pers. observ.). But within the flyway pattern of the Mississippi Valley, with abundant food supply and observed active foraging, greater body weights and vigorous behaviors occurred along with sperm release and insemination.

There is no clear explanation for the absence of cloacal sperm in migrant female Tennessee Warblers at Long Point (Fig. 2). It is possible that the sample taken there was either too small or not representative. Alternatively, perhaps the initial stimulatory factors in southern to middle United States led to an only temporary and perhaps abortive surge of mating activity.

Characteristics of males releasing sperm. Although males releasing sperm were distinguished statistically by greater body weights (Fig. 2), they did not stand out in other morphological respects from their nonreleasing brethren (Figs. 1, 3, and 4). The sperm-releasing males were however distinctive in their time of capture during the day (Fig. 6). Since the nets were a constant throughout the day, the difference between sperm-releasers and nonreleasers in capture represents either a greater number of releasers early in the day or a proportionately greater activity level of releasers at that time. A greater activity level, or lower threshold for activation, in sperm-releasing males is likely to have physiological correlates that can be tested with briefly captive individual migrants, and involve metabolic parameters and potentially priming hormones among major possibilities of interest.

Characteristics of inseminated females. Females with cloacal sperm comprised a subgroup that had greater wing and tail lengths (Figs. 3 and 4). Without other and better criteria, especially ones based upon plumage, one could mistake these larger females for males. The statistically greater prevalence of abnormal sperm in lavages from birds identified as females, as compared with those from conspecific males (Table 4) is consistent with the sexing based chiefly upon plumage characteristics. The noncongruent distributions of measurements (Figs. 3 and 4) in females with and without sperm are enigmatic, but possible explanations exist. A genetic explanation based upon possible representation by two or more different breeding populations seems unlikely since Raveling (1965) found remarkable uniformity in wing and tail measurements of samples of Tennessee Warblers from different breeding populations across the continent. An explanation based upon age-class differences remains possible, but needs more kinds of information for evaluation. According to this possibility, the female subgroup with sperm and greater wing and tail measurements would most likely correspond to females beyond their first nuptial year. It can be tentatively concluded that the distributions of measurements in males and females with and without sperm suggest that both first nuptial and older males were sperm-releasers, and that only the older females were recipients of sperm.

Mating preferences. It can be asked whether "mating preferences," in the sense of Gimelfarb (1988), were represented in disjunct occurrences of sperm among female Tennessee Warblers at Foley. This possibility could be relevant to distributions of wing and tail measurements of inseminated females (Figs. 3 and 4). But physiological factors, such as those related to reproductive and behavioral maturation may be more directly important. The extent to which female and/or male choice entered into the distribution of the migrants' inseminations within the population is theoretically (Hedrick 1988) important, but remains moot without other lines of evidence.

Adult nuptial crown colors of male and female Tennessee Warblers, primarily gray and green, respectively, are the most representative ones for wood-warbler species collectively (Burtt 1986, p. 10). One might suspect that mating preference would be manifested most clearly on the basis of such a feature as crown color in these birds. But this was not borne out by the Tennessee Warblers at Foley (Fig. 1). My results with crown color are consistent with a "neutral-mate-choice hypothesis" (Lightbody and Weatherhead 1988). I do not know, however, whether this represents the situation also on the nesting territories. Correlative cloacal lavage and other techniques at such sites during resident arrival in spring and through the subsequent breeding season should aid in answering this question.

Social factors. Quantitative relations of sperm release and insemination at Foley showed trends of interest in relation to sex. Among the males the numbers of individuals releasing sperm and the numbers releasing large numbers of sperm increased towards the end of the species' migration period through the area. Females with cloacal sperm occurred only during, or within a day of, times of capture of males releasing sperm (Fig. 5). Inseminations over all years insofar as known fell within a period of about 8 days, and could have been easily missed without frequent sampling. The brevity of this period, coinciding with the transit by the majority of males, additionally suggests the likelihood of social factors in the migrants' inseminations. If these inseminations during migration had the potential for early fertilizations, then the early and late females could have been at a disadvantage for earliest commencement of reproductive activity on the nesting territory.

Reproductive success in some of the better studied northern temperate passerines declines with the advance of the breeding season. In relation to this, there are important questions about an apparent limitation on evolution of earlier breeding dates (Price et al. 1988). My results imply that early events in passerine breeding seasons may be multiphasic and stretch out in time, starting before arrival at, and selection of the nesting site and territory, depending upon species, and perhaps population.

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