

TIMING OF SPERM RELEASES AND INSEMINATIONS IN RESIDENT EMBERIZIDS: A COMPARATIVE STUDY¹

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Abstract. Timing of cloacal sperm releases by males and inseminations of females was studied by means of cloacal lavage with six emberizid species: Northern Cardinal (*Cardinalis cardinalis*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Indigo Bunting (*Passerina cyanea*), Red-winged Blackbird (*Agelaius phoeniceus*), Brown-headed Cowbird (*Molothrus ater*), and Northern Oriole (*Icterus galbula*), near Foley, Missouri, for six consecutive years. Individual birds ($n = 921$) and their recaptures ($n = 275$) supplied 1,196 cloacal lavage sets. Usually both first nuptial and older males released sperm continuously; species differed in sperm release starting date and in relation to migration/arrival and date of first detected insemination. Monogamous species, as well as those more structured socially, had spring-early summer inseminations clustered around one or two times (insemination phases) presumably generative for first and second broods. The percentage of males releasing sperm varied by species from 82 to 100% during the year's first insemination phase, and 92 to 100% during the second. Brevity of insemination phases in most species, and their temporal proximity with laying, indicated that in these, earlier copulations are apt to be courtship-but not insemination-related. Percent of captured females with whole (fresh) cloacal sperm varied by species from 13 to 59% during the first insemination phase and 10 to 78% during the second. Results presented demonstrate the efficacy of intensive and quantitative cloacal lavage for providing data about hitherto neglected important aspects of individual and populational reproductive strategies and environmental responses.

Key words: *Emberizidae; cloacal lavage; insemination; species differences; sperm release.*

INTRODUCTION

It has been shown by means of cloacal lavages that males of many species of passerine birds release copious sperm (spermatozoa) into the cloaca during and sometimes preceding the breeding season (Quay 1984). This process when studied in short-term captives, as well as in free-living recaptures, appears to be both continuous and spontaneous, requiring neither the immediate presence of a female, nor apparent copulatory behavior (coitus) (Quay 1985a, 1987a). Support for the idea that cloacal contents of male passerines can be transferred to the female cloaca during insemination has been obtained through the demonstration of transfer of artificially instilled microspheres from male to female cloacas in free-living natural populations (Quay 1988).

Additional kinds of studies are needed in order to fully define the events and mechanisms required for, and limiting, insemination in these birds. Important questions remain, especially

concerning what and when sperm are received and taken up by females. Cloacal lavages (CLs) show sperm in passerine females as well as in males, but usually in relatively few birds at any one time during the breeding season, and usually in considerably smaller numbers (Quay, unpubl. observ.).

The present study has the immediate objective of evaluating the comparative occurrence of cloacal sperm and their fragments in six species of resident breeding emberizid passerines at a single site in Missouri. These species were selected retrospectively on the basis of three criteria: (1) relatively large numerical representation in captures with CLs during the study years; (2) pronounced sexual dimorphism, especially in plumage; (3) known differences in breeding season biology. Major subjects in the analysis of the results were: (1) timing of cloacal sperm and their fragments in females; (2) whether temporal patterns were present in these occurrences; and (3) whether and to what extent these patterns were consistent with the known scheduling of events during the breeding season of the species. Since timing of insemination depends first of all upon male release of sperm, temporal and related char-

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TABLE 1. Dates of spring-summer mist netting and cloacal lavaging at the study site.

Year	Ranges* in dates
1983	30 April-7 May
1984	1 May-14 May
1985	25 April-16 May, 27 May-1 June
1986	3 April-1 June
1987	21 May-8 June
1988	9 May-15 May

* Inclusive and continuous (daily).

acteristics of male sperm release in these same populations are presented as well.

METHODS

STUDY LOCATION AND TIMES

This study was conducted in mixed habitats at a farm about 5 km NNW from the town of Foley, Lincoln County, Missouri (39°08'N, 90°46'W). Characteristics of the study area have been noted before (Quay 1985a, 1985b).

Continuous operation of mist nets and collection of cloacal lavages occurred during spring-early summer periods for six consecutive years (Table 1). These periods varied due to factors beyond my control. But in the aggregate they encompassed the apparent time of first inseminations for each species and extended through the timing of major events affecting the first broods of the year for many of the pairs of each species. Events after the start of possible second broods, and during the terminal part of the reproductive season were not monitored.

CAPTURE AND PROCESSING

Species used and numbers of individual birds and their recaptures providing sets of cloacal lavages on slides are listed in Table 2. Captures were all by means of mist nets, and permanent marking of all birds was by numbered metal leg bands (U.S. Fish and Wildlife Service). Nets were "open" (functioning) nearly continuously but for times or anticipations of bad weather, usually at night. Nets were checked and captured birds removed at frequent intervals. Tabulation of netting efforts during 1983-1986 is available elsewhere (Quay 1987b). Number of nets and particular net sites utilized varied in part from year to year. For these and other reasons, quantitative comparisons of numbers of captures of any species or subgroup between years, and between species, are unlikely to be meaningful ex-

cept in cases of rather gross temporal species differences.

Routine preliminary processing of the birds included weighing, measuring (wing chord and tail lengths), taking of notes on plumage, sexual/reproductive characteristics, and abnormalities and pathologies if visible externally. Cloacal lavages were made according to techniques and their modifications as described previously (Quay 1984, 1986a, 1986c, 1987a).

During 1983 to 1985 number of lavages/slides per bird varied. But starting in 1986 and continuing through all subsequent years the "lavage set" made from each bird consisted of four slides. These and their preparation represent a "standardized cloacal lavage procedure" having the aim of maximizing the comparability of results from bird to bird and from time to time. The first three lavages (lavage slides) of each set or bird capture were made with minimal stimulation of the bird, and washed out essentially all sperm occurring within the cloaca at that time. The fourth or last lavage (lavage slide) directly followed a series of gentle but rapid anterior-to-posterior strokes by thumb and forefinger (or for very small birds, teflon tubing-tipped forceps or hemostat) of the skin bilateral to the vent. This had the purpose of facilitating the bringing down to the cloaca some sperm and/or their fragments that may have been in the male's glomus seminale or the female's proximal regions of the reproductive tract. All birds were immediately released unharmed after these procedures and banding.

The numbers of within- and between-year recaptures of repeatedly lavaged birds (Table 2, Figs. 3, 4, 6, 7, 9, 10) attest that the lavage procedure was harmless when performed properly and with care. This means that the pipet tip was never forced into the cloaca, since it could then puncture the cloacal lining and cause serious injury. Impaction of the cloaca with dehydrating fecal material can be progressive with time in netted birds that are held too long as temporary captives. This material has to be gently removed externally by blunt-tipped forceps and/or pipet tip before any lavages can be taken safely.

MICROSCOPY

Sperm and sperm fragments were identified, estimated in number and photographed by means of phase contrast light microscopy as previously described (Quay 1986a, 1989)(Figs. 1 and 2).

TABLE 2. Names of species^a and sources of cloacal lavages (CLs).

Subfamily Species	Males		Females		Totals		
	Individuals	Recaptures	Individuals	Recaptures	Individuals	Recaptures	CL sets
Cardinalinae:							
<i>Cardinalis cardinalis</i>							
Northern Cardinal	52	39	64	18	116	57	173
<i>Pheucticus ludovicianus</i>							
Rose-breasted Grosbeak	41	2	18	8	59	10	69
<i>Passerina cyanea</i>							
Indigo Bunting	206	42	190	25	396	67	463
Icterinae:							
<i>Agelaius phoeniceus</i>							
Red-winged Blackbird	107	11	112	17	219	28	247
<i>Molothrus ater</i>							
Brown-headed Cowbird	21	17	38	39	59	56	115
<i>Icterus galbula</i>							
Northern Oriole	44	28	28	29	72	57	129
Totals:					921	275	1,196

^a Names and sequence follow AOU check-list (1983).

STATISTICS

Comparisons of results in the form of two or more samples employed ANOVAs and the Student-Fisher *t* where appropriate, but usually had to depend upon nonparametric statistics instead. In the latter the Wilcoxon's two-sample test (Sokal and Rohlf 1969, p. 392-394) was used.

RESULTS AND DISCUSSION

COMMON FEATURES

Males. The males of all species showed long-term continuity of cloacal sperm release (Figs. 3-7, 9, 10). Starting dates differed in relation to species, as did the length of time of male sperm release in advance of the first detected inseminations of females. Generally, numbers of sperm per male lavage set were relatively low during the first days of the record. But typically at all subsequent times some, usually a majority of, males in the population sample were releasing large numbers of sperm.

Females. Four types of cloacal lavage results were found in females: (1) Lack of sperm and of sperm fragments—neither reproductive nor insemination status could be inferred from such negative evidence (note female recapture histories in Figs. 6, 9, and 10). (2) Occurrence of whole sperm—the early postinsemination type of cloacal lavage (Quay 1989). (3) Occurrence of sperm fragments—the late postinsemination type of cloacal lavage (Quay 1989). It should be noted that whole sperm can be artifactually rendered

headless in lavages by prolonged exposure to hypotonic media prior to fixation, and that sperm vulnerability to changes in tonicity can vary, but generally only slightly if the standardized lavage procedure is followed without interruption. (4) Simultaneous occurrence of both whole sperm and sperm fragments—representing both recent (probably within the day of capture and lavaging; = early postinsemination) and earlier (probably by a few days to several weeks; = late postinsemination) insemination.

Occurrences of whole (complete) sperm in females were brief. These events characterized particular days and probably did not extend to adjacent days unless additional insemination(s) occurred (cf. Indigo Bunting recapture females E, G, and J, Fig. 6, upper panel; Northern Oriole recapture females A and B, Fig. 10, upper panel). Exceptions were most probable in the female Brown-headed Cowbirds, the species having the greatest percent occurrence and probable frequency of inseminations (Fig. 9, upper panel). This short, likely about 1-day or less, term of detectable postinsemination cloacal sperm, is consistent with the time interval noted for detection of microspheres transferred from male to female cloacas (Quay 1988).

Sperm fragments (Fig. 1) in female cloacas can be expected to represent the result of longer-term sperm residence within the female tract, with gradual breakdown of the inseminated sperm. Examples of relatively short postinsemination intervals (one to several days?) for cloacal sperm

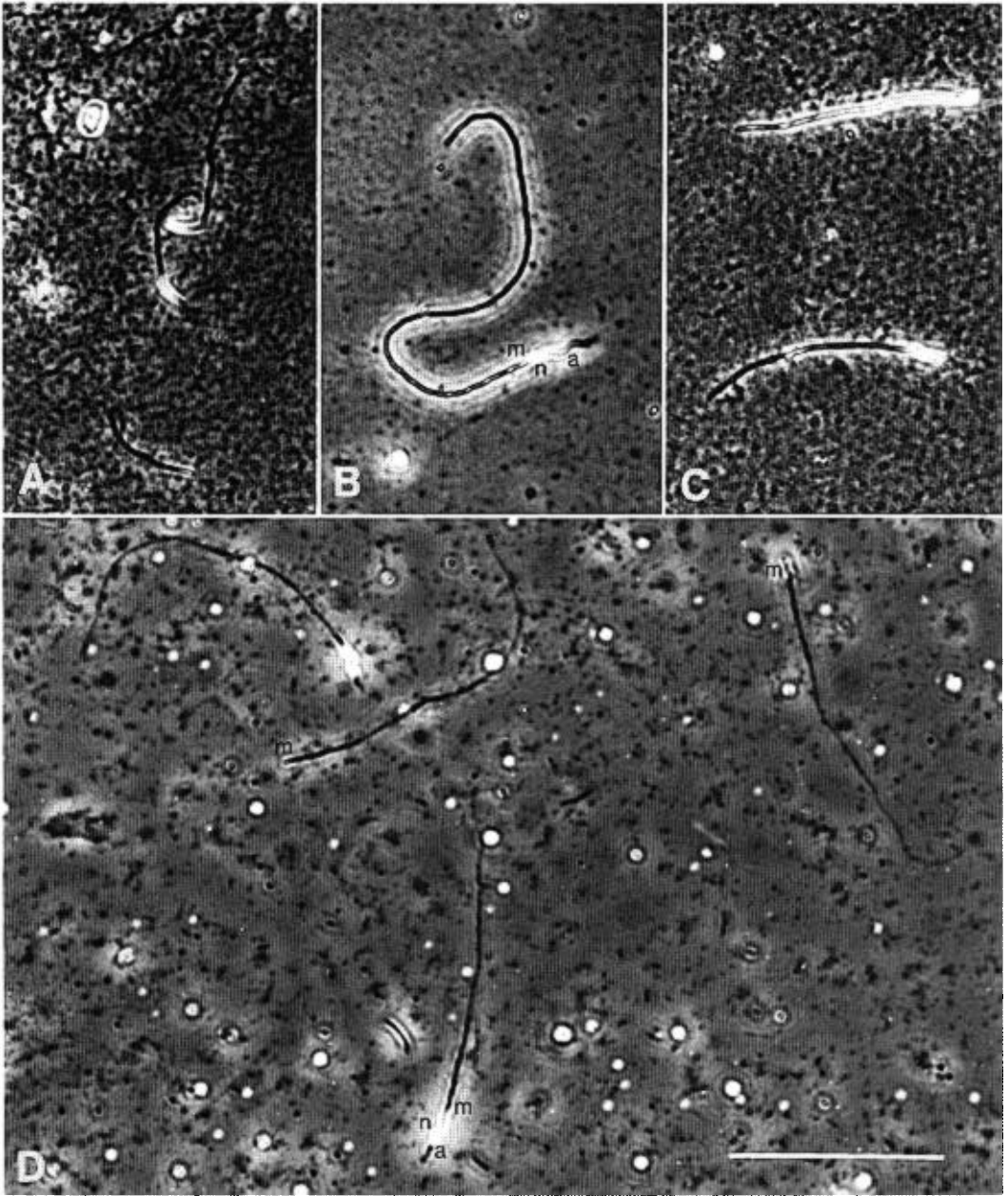


FIGURE 1. Photomicrographs (at same magnification) of sperm in cloacal lavages from female emberizid specimens in this study. A. Northern Cardinal, 10 May 1988; headless sperm fragment at bottom has middle-piece; two at center have heads as well; this is the sole female of this species having both whole sperm and sperm fragments in a lavage set (Fig. 3, upper panel). B. Indigo Bunting, 10 May 1986, sperm with complete acrosome (a), head (h), and middle-piece (m); tail's truncation probably due to FFA (fold-fusion anomaly). C. Brown-headed Cowbird, 11 May 1988; two sperm with truncated tails (at left) and abnormal and/or damaged heads (at right ends); both lack an acrosome; spiral configuration of head remains only in the lower spermatozoan. D. Northern Oriole, 10 May 1988; four sperm, all with essentially complete tail principal-pieces; two have acrosome (a) and head (h) as well as middle-piece (m), and two have middle-piece (m) but have lost head and acrosome. The scale bar = 50 μ m.

fragments were suggested near the times of the first inseminations of the season in Indigo Buntings (Figs. 5 and 6) and Brown-headed Cowbirds (Fig. 9). These chart records and other observations are consistent with the interpretation that females of these species are subject to more frequent inseminations and that there may be more spill-over or rapid turnover and voiding of inseminated sperm. Actual existence and dynamics of this needs to be tested.

Examples of relatively long postinsemination intervals (about 3 to 4 weeks?) for cloacal sperm fragments are seen in Northern Cardinals (Fig. 3) and Red-winged Blackbirds (Fig. 7). In passerines this long interval plausibly represents the period during which viable sperm are retained by the female. Sperm-storage "glands" of the oviductal and/or uterovaginal regions of the female reproductive tract are the best-, but still little-, known sites involved in this. Although most often studied in domesticated galliform birds (Van Drimmelen 1946, Bobr 1962, Fujii 1963, and others) sperm storage glands have been either observed or inferred in several feral birds of other taxa (Hatch 1983), including two of the passerine species in the present study, the Red-winged Blackbird and Indigo Bunting (Bray et al. 1975, Shugart 1988). Furthermore, prolonged (28 to 68 days) sperm storage has been demonstrated among passerines, in domesticated Common Canaries (*Serinus canaria*) (Birkhead 1987) and free-living Red-winged Blackbirds (Bray et al. 1975).

It is likely that late release of sperm fragments into the passerine female cloaca represents at least in part the fate of some of the sperm contained in sperm balls (Fig. 2) and released higher in the female reproductive tract. This, and the likely contributions of sperm balls in sperm storage and sperm competition (Quay 1986b), follows from and is consistent with the frequently observed late cloacal voiding of compressed and sperm-depleted sperm balls by female passerines.

SPECIES CHARACTERISTICS

The following sections describe species characteristics and differences observed here in the timing and occurrences of sperm releases and inseminations. They also discuss relationships possible between the times of insemination and female sexual and reproductive characteristics. Data for these considerations are drawn from my obser-

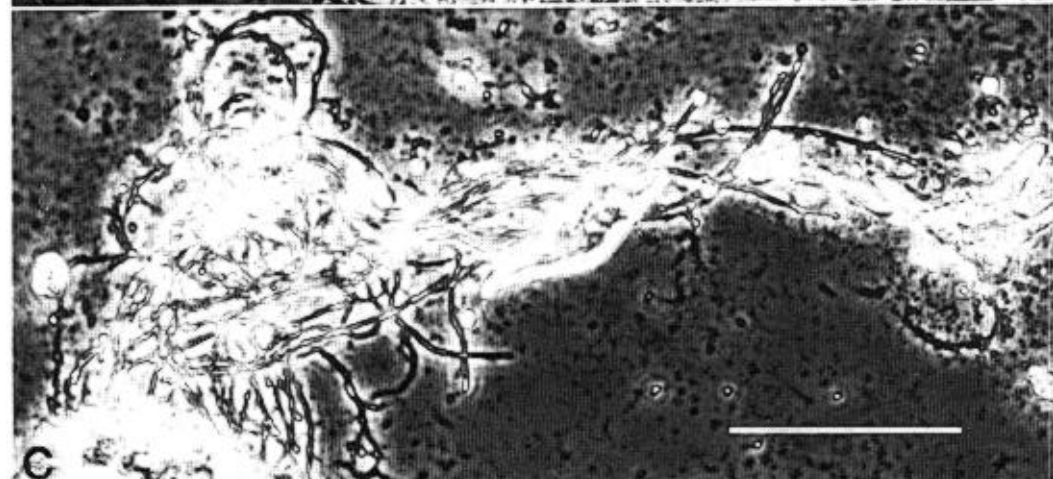
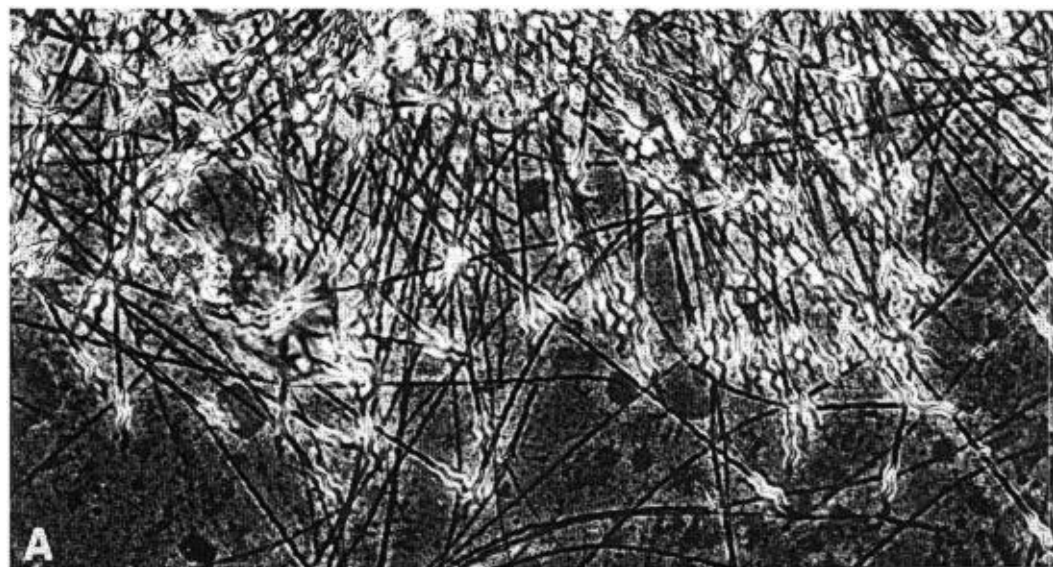
vations on these populations, and from literature concerning the respective species. Two general categories of information are utilized: spring arrival dates and associated behaviors, and sexually or reproductively related features of the birds, their changes and apparent scheduling of change. Direct personal observational data on laying and fledging were slight under the demands on time made by the primary objectives of the study.

NORTHERN CARDINAL

Arrival and start of events. At least some of the cardinals were year-round residents in the general region of the study. Territorial behavior was seen in the first days after my arrival in April 1986. At Nashville, Tennessee, 320 km south of my study area, cardinals have been reported to begin taking territory and choosing mates in late February (Laskey 1944). About half of my males were releasing sperm by the first week in April (Fig. 3), some in large numbers (6.0×10^4 to 2.4×10^5). This was 12 to 15 days before the first detected female insemination (Fig. 3).

Possibly unique to this species, among those studied here, was a pause in sperm release by two males during what appeared to be incubation and nestling periods (30 April to 10 May, Fig. 3, lower panel). Further study of this possibility is needed.

Inseminations. Early postinsemination lavages of females were from 19 to 30 April. Times of day at which capture occurred of females with cloacal sperm did not differ significantly from those of females without. One female ("A," Fig. 3) was inseminated at least twice. At the first insemination (19 April) there was no brood patch but thinning of breast feathers had denuded a central area 13 mm in maximum diameter. At the second recorded insemination (26 April) a week later, the brood patch was near full size (33 mm maximum diameter) and had a near intermediate (code ++) degree of edema. This pattern of change was representative of the chronology of brood-patch development in freshly inseminated birds. The female inseminated on 30 April had a near maximally (code +++) edematous brood patch of full size. Therefore, brood-patch development and activation occurred within the first insemination phase. Vent walls and lips of these birds were somewhat



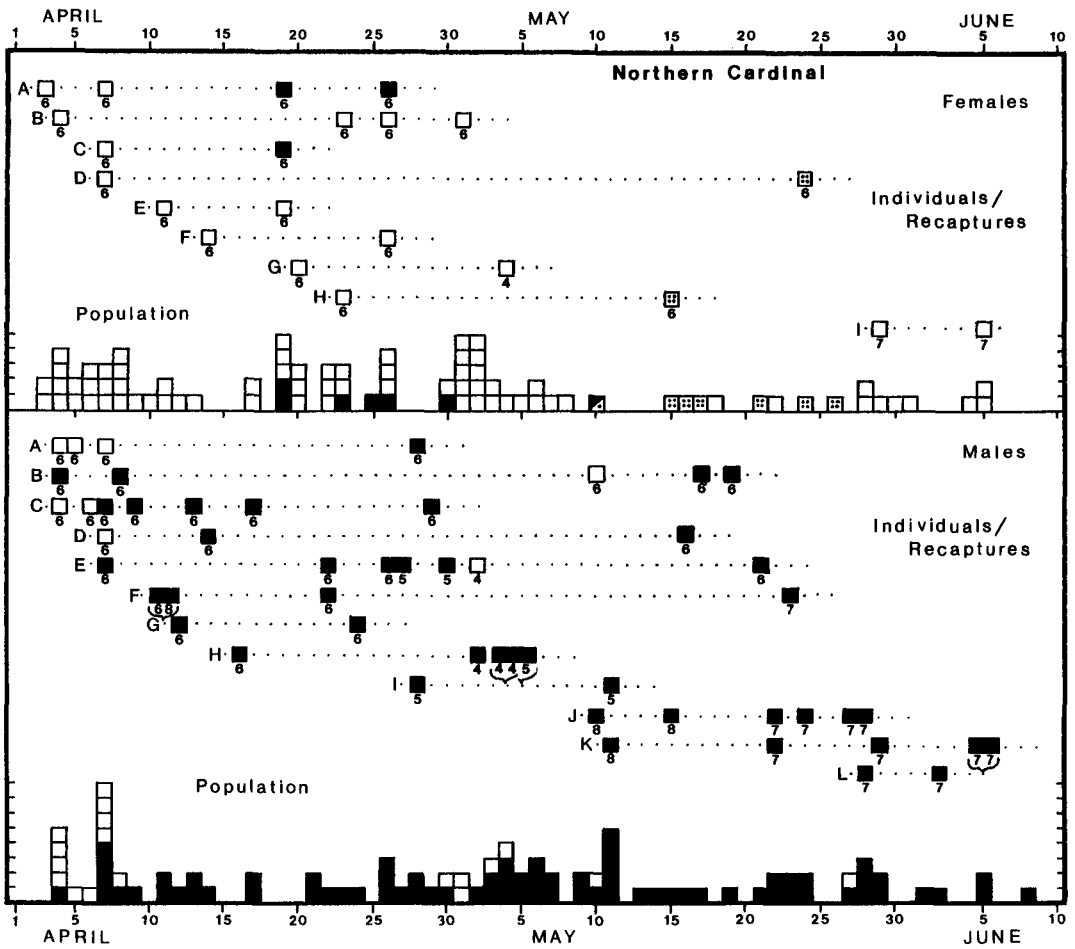


FIGURE 3. Chart of cloacal lavage sets from Northern Cardinals at Foley, Missouri. Black squares or half squares represent lavage sets containing whole sperm (early postinsemination). Dotted squares or half squares represent lavage sets containing sperm fragments (late postinsemination). Numbers under the squares are the last digits of the year; brackets under some years indicate duplication and/or shift of calendar day record. For example, female A was captured and lavaged four times, all in 1986; male F was captured and lavaged four times, twice in 1986 and once each in 1987 and 1988. The records of five additional females captured and lavaged twice without showing sperm are omitted from the "Individuals/Recaptures" in the upper panel.

thickened but the vent itself was prelaying in diameter and other characteristics.

Sperm fragments. Female cloacal sperm fragments occurred 15 to 26 May, thus averaged about 27 days after the middle of the period

containing most inseminations. Females voiding sperm fragments all had brood patches of full size and sharply demarcated edges. However, they varied from near maximum edema (++++) and hyperemia (++++) to distinctly regressive

←

FIGURE 2. Photomicrographs (at same magnification) of parts of sperm balls in cloacal lavages from emberizid specimens in this study. A. Male Indigo Bunting, 11 May 1984; edge of sperm ball showing typical outward orientation of normal sperm, with complete acrosome and head (cf. Fig. 1B). B. Female Indigo Bunting (= I in Fig. 6, upper panel), 29 May 1986; medium-sized sperm ball greatly depleted of sperm, and those remaining have lost acrosome and head, but usually have retained the middle-piece. C. Female Rose-breasted Grosbeak, 9 May 1988; small noncompacted sperm ball mostly depleted of sperm, and those remaining have missing or damaged heads. The scale bar = 50 μm.

states (++) and (++), respectively) with yellowing. Vents of these birds varied from recent to regressed postlaying types. These circumstances are in harmony with timing of sperm fragment voiding near or around the approximate time of fledging. The female (Fig. 3, 10 May) with both early and late postinsemination lavage characteristics was anomalous and may represent a case of nest failure (Scott et al. 1987) or some other problem; its vent was small and either prelaying or fully regressed in size.

If we assume that laying commenced within a day or so of insemination, 27 days from insemination extended to the time of expected fledging nest departure (Burns 1915, Laskey 1944, Ken-deigh 1952, Harrison 1978). Female physiological changes at this time thus appear to have been associated with release of at least some of the sperm stored in the reproductive tract, with their fragmentation and voiding.

Later events. Cardinals are multibrooded; four broods per season have been reported (Laskey 1944, Bent 1968). Lack of apparent fresh inseminations at the time expected for the start of a second brood differs from what was observed for the other five species studied here. It is possible, but not proved, that cardinal sperm stored from earlier, first brood, insemination(s) might be effective in second or later brood fertilizations. However, in the local circumstances of this study, second or later broods may possibly not have occurred. By mid- to late summer during the study years cardinals deserted major upland portions of the study area, probably because of drought and poor foraging conditions. Nesting success in this species has been correlated with "understory foliage and arthropod biomass in territories" (Conner et al. 1986).

ROSE-BREASTED GROSBEAK

Arrival and sperm release. First males at the study location, 26–27 April, were within the time frame of the usual arrival dates for this sex in the St. Louis region, 22–29 April, in early records (Widmann 1907). Also it has been reported that first male arrivals in the spring appear to be those that stay to breed (Dunham 1966). My first male, in age post-first nuptial year, had a cloacal sperm index (CSI) of 1.5–2.0 ($= 1.5 \times 10^3$ to 6.0×10^4 sperm/lavage set). Two males lavaged on 27 April (Fig. 4) were in their first nuptial year; one lacked

cloacal sperm; the other had a CSI of 1.0 ($= 1$ –10 sperm/lavage set).

The above evidence of sperm release by newly and first arrived males is consistent with the finding of low levels of sperm release in migrants as far south as Galveston, Texas (Quay 1985a). By 2 and 5 May at the Foley study area both first nuptial and older males had CSIs of 2.5–3.0 ($= 2.4 \times 10^5$ to 6.0×10^5 sperm/lavage set) and these often included sperm balls (Fig. 2). The first detected inseminations of females, 4–6 May (Fig. 4), were at this time. Therefore within the 7 to 9 days after arrival males had markedly greater sperm outputs and were inseminating females (Fig. 4). Occasional males with lavages lacking sperm (Fig. 4, lower panel) included both first nuptial and older individuals, as did those having lavages with sperm. It will be important to ascertain whether mate bonding is a critical factor in this difference.

Female characteristics and inseminations. Female Rose-breasted Grosbeaks have been reported to follow males by a few days in their spring arrival times at this latitude (Butler 1897, Widmann 1907, Dunham 1966); my observations agree in part (Fig. 4). However, at Galveston as well as at Foley, males with cloacal sperm were individually each attended closely by a female. Males without cloacal sperm did not have an evident female consort (Quay 1985a). Behaviors observed in the present as well as the earlier study support belief in pair-bonding of sperm-releasing males prior to arrival at the nesting territory. Nevertheless an interval of a few days at the nesting area was necessary prior to high sperm counts in males and inseminations of females.

First spring inseminations of females were clustered in the period 4–9 May, and at least some females were inseminated at least twice during this period (females B and C, Fig. 4). Repeated copulations have been observed in the "courtship ceremonies" of semicaptive pairs (Ivor 1944, Dunham 1966), but timing with respect to laying was not indicated. Copulations of two of Dunham's females occurred during the time of nest building.

Brood patches of my females inseminated 4–9 May varied from absent (code 0) to full size (48 mm maximum diameter) with marked edema (+++) and notable hyperemia (++) but without correlation with date except in the case

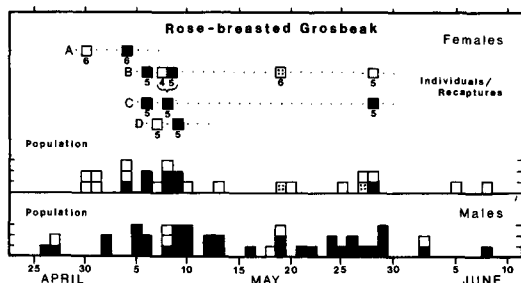


FIGURE 4. Chart of cloacal lavage sets from Rose-breasted Grosbeaks at Foley, Missouri. Symbols, letters, and numbers are keyed as in the legend for Figure 3. Six males with recaptures (one each) are not shown in an "Individuals/Recaptures" section of the lower panel; the two of these (both post-first nuptial year) that were lavaged were releasing sperm (i.e., 12 May 1984, and 8 May 1985; 9 May 1986, and 10 May 1988).

of recaptures (B and C, Fig. 4). A second period of insemination was suggested (female C, Fig. 4) about 3 weeks later; but data are deficient for confident conclusions. This female at this time had a maximally developed (+++++) and extremely edematous brood patch, and a postlaying vent. It was likely to have recently completed the incubation and nestling periods of its first brood (cf. Burns 1915, Ivor 1944, Bent 1968). Females voiding sperm fragments at about the same time (27 May) or much before (19 May) this time, also had full-size and edematous (++++ to +++) brood patches and large vents. This species is variously characterized as single- to double-brooded (Bent 1968, Rothstein 1973, Harrison 1978), and the 28 May insemination could have represented the beginning of a second brood for female C (Fig. 4). Potentially more complex timing scenarios are possible in this species, known for occurrence of overlapping first and second nestings (Rothstein 1973).

The time interval for selection and establishment of a territory, along with nest building, therefore seems brief (probably 4–9 days) in this species, especially if insemination precedes egg laying by only a day or so, and if, as in some species, nest-building activities markedly decline a day or two before the first egg is laid (Collias and Collias 1984, p. 273). However, in a semi-captive Rose-breasted Grosbeak the entire construction of a nest has been reported to have required only about 2 days, and an egg was laid in it on the day before it was completed (Ivor 1944).

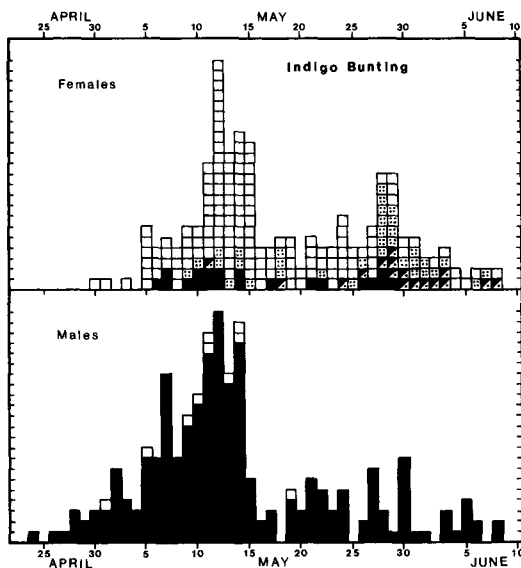


FIGURE 5. Charts of cloacal lavages from the female and male populations of Indigo Buntings at Foley, Missouri. These include recaptures (shown in part in Fig. 6) as well as once-only captures/lavages. Symbols are keyed in legend for Figure 3.

INDIGO BUNTING

Arrival and sperm release. Early (24–30 April) arriving males and all subsequently recaptured males were releasing sperm (Figs. 5 and 6). About 70% of the older (post-first nuptial) males and all first year (first nuptial) males during these early dates were releasing sperm in numbers almost certainly too low (CSI 1.0; $\approx < 10$ sperm/lavage set) for effective insemination. But very quickly, even by 1–3 May, about 60% of males of both age classes were releasing sperm in sufficient numbers (CSI 2.0–3.0; $= 6.0 \times 10^4$ to 6.0×10^5 sperm/lavage set) to be potentially effective in inseminations. This conclusion is supported by the transfer by bunting males having such CSIs of cloacal microspheres (Quay 1988) to females in this population. By the second and third weeks of May male Indigo Buntings, mostly but not exclusively first-year birds, were inseminating females as affirmed by their simultaneous transfer of instilled cloacal microspheres (Quay 1988).

The 10 males that had no cloacal sperm (Fig. 5, lower panel, six first-year and four older birds) were captured once only. They seemed to be centered in the first period of abundant insemina-

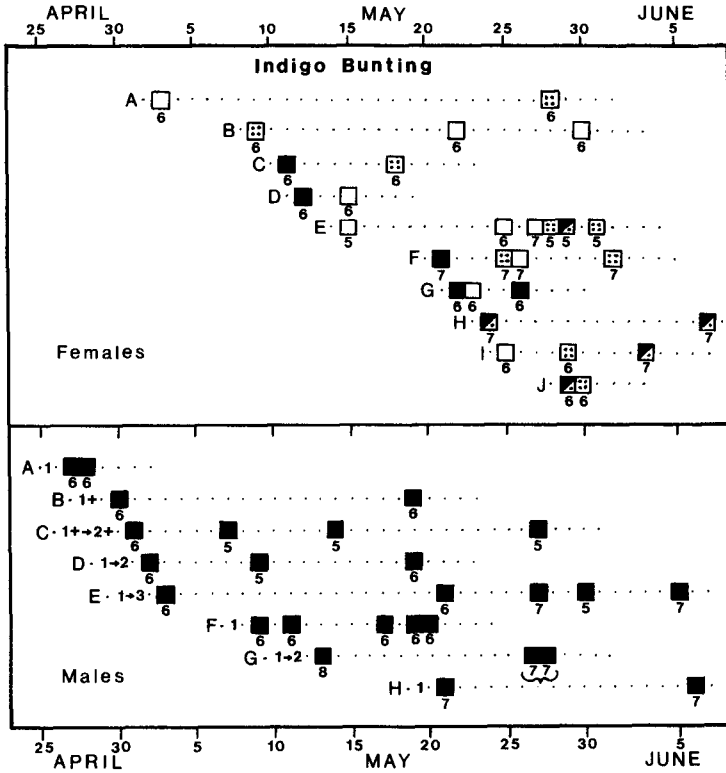


FIGURE 6. Charts of cloacal lavage sets from a selected number of the female and male Indigo Buntings that were recaptured and relavaged. These are included in the total population charts (Fig. 5). Symbols and numbers under the symbols are keyed in the legend for Figure 3. In addition, the numbers immediately following the letter (A–H) designation of a particular male (lower panel), or (A–J) designation of a particular female (upper panel), give the age(s) (nuptial year[s]) on the basis of plumage characteristics and/or recapture history represented by the charted data. Thus male A was in its first nuptial year when twice captured and lavaged in 1986; male C was beyond its first and second nuptial year(s), respectively, in 1985 and 1986 when first, then subsequently, captured and lavaged. An additional 11 females and 17 males that were recaptured/relavaged one or more times are not shown here. Most (10/17) of these omitted males were first nuptial transients captured/lavaged two or more times within a period of 2 to 3 days, chiefly in 1986. All of these and other recaptured males were releasing sperm at all times that they were first or later captured and lavaged.

tions and that of numerous transients and/or floaters in the population (Fig. 5). It is not known whether these birds were sterile, or—more likely, later migrants going still farther to their nesting grounds, and not yet releasing sperm. Whatever the correct characterization may be of subclasses of this wave of Indigo Buntings, the magnitude of this wave was unique to this species (cf. Fig. 5 with Figs. 3, 4, 7, 9, 10) and may have significance in the provision of greater diversity in the potentially available gene pool, particularly for the first brood.

Inseminations. Inseminations were nearly continuous from 6 May to at least 8 June, but with the suggestion of two peak periods, 6–14

May and 26 May–3 June (Fig. 5, upper panel). Occurrences of sperm fragments in lavages from females also were suggestive of two periods. The first of these lagged by a few days the peak in fresh inseminations and may have conceivably represented an overflow or excess or turnover from sperm holding capacity of the storage mechanisms of the female reproductive tract. The second peak in cloacal sperm fragments coincided with the second peak in inseminations, and, as in the two previous species, is likely to have represented the timing of the start of second broods by residents.

The less structured or messier appearance of the timing of inseminations in this species as

compared especially with the monogamous Northern Cardinal (cf. Figs. 3 and 5, upper panels), is likely to be mostly the result of the variable mating systems and less effectively regulated (restricted?) opportunities for insemination in the Indigo Bunting. Besides the natural occurrence of polygyny, to the extent of involving 15% of the males, four other mating system types or subtypes have been described in this species (Carey and Nolan 1975, 1979; Payne 1982; Westneat 1988): (1) season-long monogamy, (2) successive monogamy—male mated to two or more females without overlap in the timing of respective association, (3) short-term monogamy—male mated to a single female for less than the entire breeding season, and (4) unmated—male forming no pair-bond during his residence, most commonly in first-year birds (Carey and Nolan 1979). Added to this is the complexity fostered by extra-pair copulations (or inseminations) in this species (Westneat 1988). The transfer of cloacal microspheres from three different males to one female in my population, 12–13 May, may have represented extra-pair inseminations (Quay 1988). But strict characterization of these is not possible in the absence of knowledge about the pairing status of any of the participants.

The 21 female Indigo Buntings inseminated during the first period of such activity (6–15 May, Fig. 5, upper panel) had no external signs suggesting the approach of reproductive activity, in contrast with early inseminated females of the preceding two species. Also, the time of day of capture did not differ between females with fresh cloacal sperm and those without. Eighteen of these freshly inseminated 21 females were examined for brood-patch development. No signs were present beyond possible very slight thinning of breast feathers medially (1 to 6 mm maximum diameter of bare area). The vent was small and its lips slightly if at all thickened. However, by 4 days (May 19) following the first insemination period, female buntings, even those now not showing cloacal sperm, had maximally developed brood-patch size (28 mm maximum diameter) with sharp boundaries, beginning edema, and notable hyperemia. Maximal activity (edema + hyperemia) as well as size occurred in female buntings near and at the period of second major insemination activity (26 May–3 June), probably typically near the end or following incubation and nestling phases of the first brood.

RED-WINGED BLACKBIRD

Arrival. The study area's Red-winged Blackbirds probably wintered appreciably farther south, towards and within the Gulf states (Bent 1958, Meanley 1965, Nero 1984). A female that I banded and lavaged in the study area 26 April 1986 was recovered 13 February 1988 near Jennings, Louisiana, about 65 km from the Gulf of Mexico. Some males and fewer females had arrived in the study area by the end of the first week in April. One each of the first two male arrivals and the first two female arrivals that were lavaged (5 and 9 April, respectively) were resident birds that were each present for at least three sexually active consecutive years (Fig. 7).

Sperm release. Males were soon active in setting up territories, but were not releasing sperm until about a week after the first noted arrivals. Also both first nuptial and older birds appeared to be about equivalent in levels of lavage sperm and continuity of sperm release. Sperm release was continuous through the breeding-nesting season in all recaptured and relavaged birds. But by 6 June one previously releasing male (in age 2+ years) had stopped releasing sperm and no new inseminations of females were noted. This probably related to relative desiccation and poor foraging in the upland environs of the focal pond habitat and nesting of these birds at this time.

During the first week of sperm release (13–19 April) numbers of lavaged sperm were already up to levels (CSI 2.0 to 3.0) consistent with effective insemination and were accompanied by small- to medium-sized sperm balls. This was true for both first nuptial and older males (based upon plumage characteristics, Selander and Giller 1960, Searcy 1979, Nero 1984), and did not reflect the lag in, and smaller size of, testes in first-year Red-winged Blackbirds reported in some other populations (Wright and Wright 1944, Payne 1969, Wiley and Hartnett 1976) nor with the significantly lower testosterone levels found in such birds (Beletsky et al. 1989). Although these first nuptial males often have been called "subadults" in the literature and are sometimes stated to not breed until the following year, observationally they often have been accredited with trying to occupy territories and breed during the first year, whether successfully or not (Wright and Wright 1944; Beer and Tibbits 1950; Nero 1956, 1984). Among my males there was marked individual variation in numbers of lavage sperm

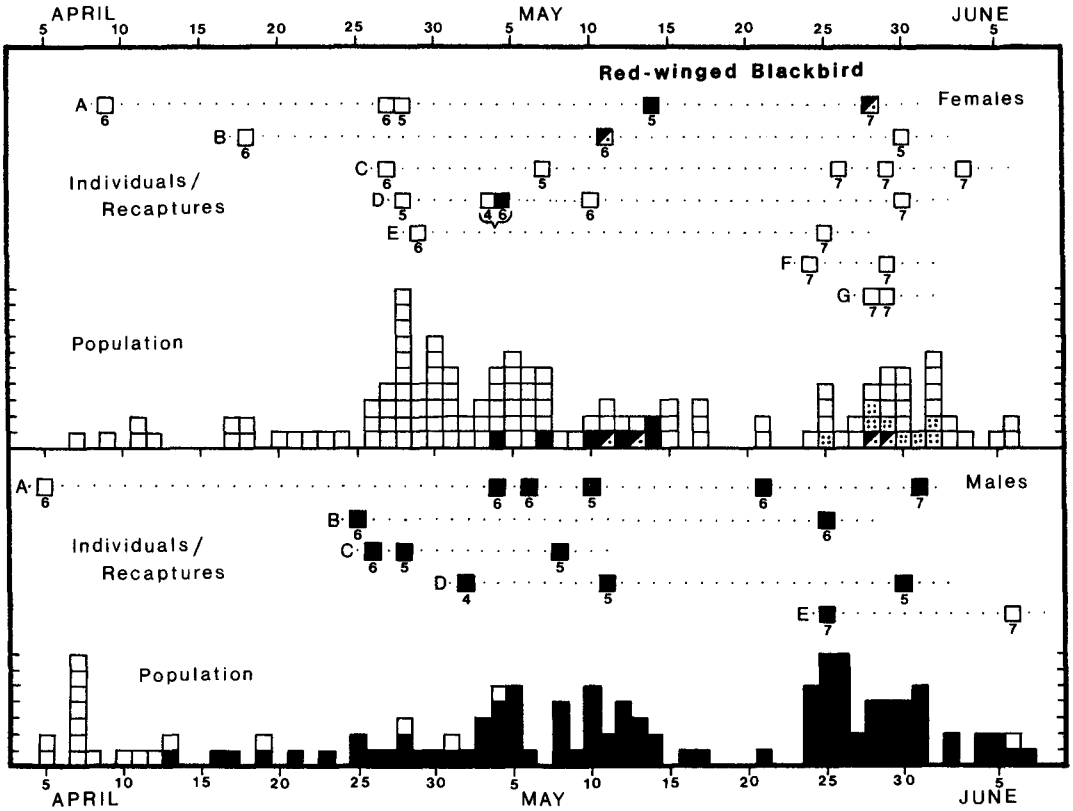


FIGURE 7. Chart of cloacal lavage sets from Red-winged Blackbirds at Foley, Missouri. Symbols, letters, and numbers are keyed as in the legend for Figure 3. The "Individuals/Recaptures" record of one female (no cloacal sperm nor sperm fragments in each of three lavage sets, 1985-1986) is omitted.

during the breeding season, and data analyses have not as yet been successful in correlating such differences with age or other factors.

It remains distinctive for the Red-winged Blackbird, however, that some males were releasing sperm in functionally significant numbers as long as 22 days before the earliest date for an insemination of a female (Fig. 7). This was far in excess of the analogous interval in the other species studied here. The red-wing's early occupation of territories and early testicular functional maturation have been repeatedly interpreted to provide an advantage in terms of ability to mate with the first females that are receptive or that are in a breeding condition. It appears more likely that such early spermatogenesis and sperm release may be at first secondary to hormonal and other physiological mechanisms important early for providing the basis for early selection of territory and its protracted advertisement and defense, strategic for the acquisi-

tion of one or more mates. A long plateau in blood testosterone levels in male red-wings has been reported during the period when most nests are initiated (Beletsky et al. 1989).

Inseminations. Sperm and sperm fragments were present in female Red-winged Blackbirds during two periods (Fig. 7), as in Northern Cardinals and Rose-breasted Grosbeaks, and less distinctly Indigo Buntings. Since more information has been published about timing of red-wing breeding behaviors, a less tenuous scenario can be suggested for the timing of insemination in this species. Here, as in the previously considered species, there is evidence of a lowered female capture rate between the insemination periods. Much of this is likely to correspond to the incubation period, when marked reduction in female activity occurs, augmented by the fact that the female red-wing is solely responsible for incubation (Nero 1984). Another, yet sharper, temporal reference point in the red-wings' schedule

is the laying of the last egg, especially of the first clutch, giving rise potentially to the first brood of the season. Payne (1969) has reported that copulation continues in this species through the nest-building period, variously timed as 1 to 8 days (Payne 1969, Nero 1984), and up to the day before the last of the usual three to four eggs are laid. With commonly 1 day between nest lining and the laying of the first egg (Payne 1969), the total expected period of copulations for a female at the start of the breeding season would be from 4 to 12 days. Lengths of the copulatory period within two California colonies have been charted as 3 to 6 weeks (Orians 1961). Both in studied western and eastern red-wing populations approaches to synchrony of the breeding activities of individuals are greater in smaller and upland populations such as the one studied here. With reported lengths of incubation and nestling periods as 11 to 14 and 10 to 11 days, respectively (Allen 1914, Payne 1969, Searcy 1979, Nero 1984), the total is equivalent to a little longer than that (18 to 21 days) from times within the first to corresponding times within the second period of cloacal sperm (Fig. 7, upper panel). This fosters the suggestion that the second insemination period and the voiding of sperm fragments from the first insemination period occurred at about the time of fledging of the first brood. The above timing sequence is approximately congruent with what occurred for a clutch of four eggs followed at the study site in 1985.

During the period of first inseminations, for the first presumptive broods, 4–14 May (Fig. 7), those females with cloacal sperm tended to be captured towards the end of the day, in comparison with females lacking cloacal sperm (Fig. 8, upper panel). At the time of the second inseminations, 25 May–1 June, there was no evidence of association of sperm or sperm fragment occurrence with time of day (Fig. 8, lower panel). It is known that laying by female red-wings occurs early in the morning, usually shortly after sunrise (Muma 1986). Copulation in red-wings has been observed through nest building and laying until the day before the last egg is laid (Payne 1969). Insemination of my female red-wings appeared to start later (cf. Nero 1956, Payne 1969) and to be centered on days just before days of laying. This implies that inseminations may have occurred with only the later copulations, and that the earlier copulations may have had chiefly or solely behavioral importance, as in part of the

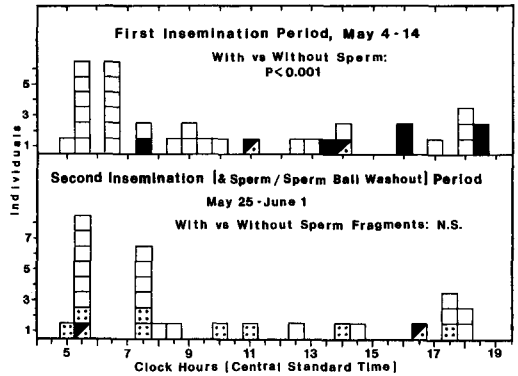


FIGURE 8. Times represented by captures of female Red-winged Blackbirds with and without sperm and/or sperm fragments in the study area. Symbols as in the legend for Figure 3. Significance of differences in temporal distributions was based upon Wilcoxon's two-sample tests (two-tailed). N.S. = not statistically significantly different.

courtship or pair-bonding scenario. A female with fresh cloacal sperm at about 17:00, 12 May, also had a palpable large egg in the lower tract, again indicating a close temporal relationship between insemination and laying.

Development of brood patches was not associated with cloacal sperm during the first insemination period. The first three (4–10 May) recently inseminated females lacked brood patches and those following (11–14 May) had partly to fully developed ones (36 to 41 mm maximum diameter) with intermediate to advanced (+ + + + +) edema and (+ + + + +) hyperemia. Both first nuptial and older (after first to after third nuptial) females represented these conditions early and late during the first insemination period. Neither insemination times nor relative timing and degree of brood-patch development were consistent with reports that younger females tend to nest and be reproductively active a little later than older ones (Allen 1914, Case and Hewitt 1963, Payne 1969, Blakley 1976).

During the second period of insemination (25 May–1 June) only two females had fresh sperm, but 10 had sperm fragments (Fig. 7). Two of the latter had disintegrating and sperm-depleted sperm balls in the cloaca. These and at least most sperm fragments associated with these, are interpreted as voided remains from the first insemination period. Brood patches of all females, with or without sperm and sperm fragments, during

the second insemination period were well developed and usually with moderate to extreme edema and hyperemia. Vent size varied greatly. One female with both fresh sperm and sperm fragments in the cloaca, had a large and flaccid vent and palpable lower abdominal egg (at 17:24), indicating that at least in this bird laying temporally consistent with that of a second brood probably occurred. During the second insemination period about 17% of captures of females with cloacal sperm and/or fragments, and about 31% of those lacking sperm and/or fragments, were captured 0.05 to about 2.0 km away from nesting areas around the ponds. During the first incubation all female red-wing captures were in the vicinity of the ponds, although especially during the preceding nest-building period some from the local population were seen gathering materials up to about a kilometer away. During the second insemination period female weights were not significantly lower than during the first one (means \pm standard errors: first period with sperm = 41.9 ± 1.1 g, without sperm = 40.5 ± 0.6 g; second period with sperm/fragments = 39.9 ± 1.2 g, without sperm/fragments = 39.9 ± 0.6 g). Nevertheless, the observed wider foraging and slightly lower body weights during the second period are in harmony with the relatively drier conditions of the upland habitats at this time.

BROWN-HEADED COWBIRD

Sperm release and male behavior. Brown-headed Cowbirds were seen and heard, generally high in trees, at the study locale at the time of my arrival on 3 April; both sexes were present already (Fig. 9). One of two males netted on the first capture day, 5 April, lacked cloacal sperm, and this was the only one lacking such sperm in the entire study (Fig. 9).

Males that were captured and lavaged through April 25 had only small numbers of cloacal sperm (CSI \approx 1.0 to 1.5; $<$ about 1,500 sperm/lavage set). However, already on 17 April a female had been inseminated, possibly by a more net-wary male, and one having more effective sperm numbers. Starting on 25 April, nevertheless, some males had relatively great numbers of cloacal sperm (CSI 2.5–3.0; = 2.4×10^5 to 6.0×10^5 sperm/lavage set), and this continued through about the middle of May. Up to about this point males were occasionally seen to be attentive of females and were often seen within 100 m or so of them. By near mid-May male Brown-headed

Cowbirds began to be much less seen and were seldom netted. This was not apt to have been due to improved net-awareness, since during the two most recent years nets were not put up until about this time (Table 1), and females were captured and recaptured during all years and during all periods during which nets were in operation. It thus appears that male behavioral emphasis shifted before mid-May (Fig. 9, lower panel).

Inseminations. If this was true, it is especially interesting that females continued to show new and repeated inseminations from late April to the beginning of June (Fig. 9, upper panel). From 15 April to 15 May 59% (30/51) of the females had fresh cloacal sperm and from 15 May to 5 June this was true for 78% (18/23). These are the greatest percent occurrences of fresh cloacal sperm in any of the emberizids studied here. Also cloacal sperm fragments occurred at about the same high level from beginning to end of the season and not just during some late phase of it, again contrasting with the situation in the other species. There was also, as might be expected with nest parasitism of diverse species, no reflection of brood timing in the spacing of either fresh inseminations nor of cloacal voiding of sperm fragments and depleted sperm balls.

Records of "Individuals/Recaptures" (Fig. 9, upper panel) show that all female Brown-headed Cowbirds captured and lavaged more than twice had evidence of having been inseminated two or more times during the season. One had fresh cloacal sperm each of the six times she was lavaged, from late April to late May over a 4-year span of the time (1985–1988), and had each time as well cloacal sperm fragments from one or more earlier inseminations (e.g., female "I," Fig. 9, upper panel).

Female Brown-headed Cowbirds can lay up to an egg a day (Payne 1965), more within a breeding season than other studied North American passerine females, and averaging 40 eggs in 8 weeks (Ankney and Scott 1980, Scott and Ankney 1980). Further, during late May and early June, the time of suggested availability of host nests at their Ontario study area, these investigators found that the cowbirds' laying rate did approach an egg per day. Therefore, it seems appropriate to ask whether the observed intensive and continuous insemination of such cowbird females (Fig. 9, upper panel) is obligatory for near daily fertilization of the eggs, especially if sperm storage occurs in females of this species. On the other

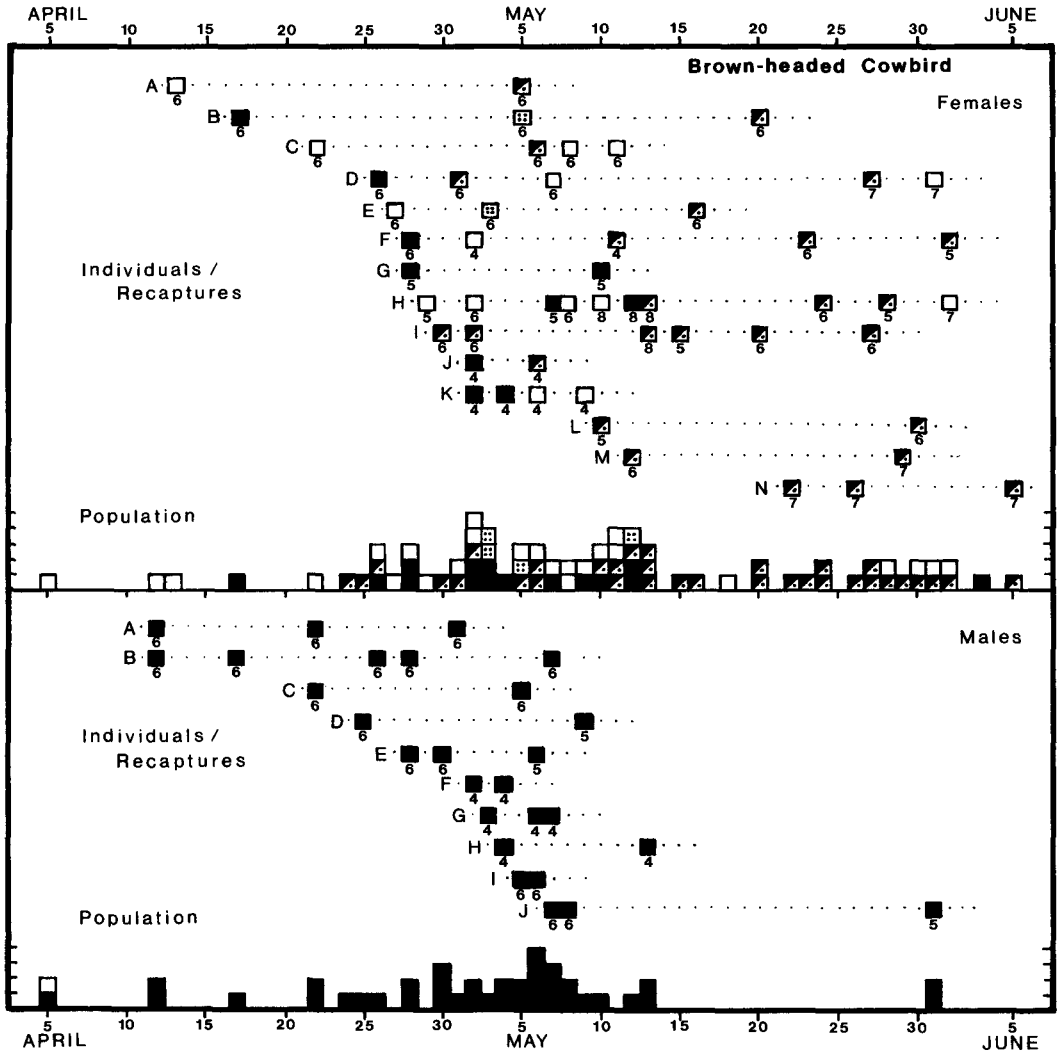


FIGURE 9. Chart of cloacal lavage sets from Brown-headed Cowbirds at Foley, Missouri. Symbols, letters, and numbers are keyed as in the legend for Figure 3.

hand, the importance of these frequent inseminations possibly should be sought in the context of sperm competition; evidence about this needs to be obtained.

My female cowbirds with fresh cloacal sperm did not differ from those lacking cloacal sperm and/or with sperm fragments only, in relation to temporal distribution during the day, from 05:00 to 19:30 (CST). However, Brown-headed Cowbird laying is reported to be early in the morning (Hann 1941), and if the degree and effects of such an approach to synchronization are like those of red-wings (see above and Fig. 8), one would expect

to see evidence of preferred timing of insemination in this species too.

Copulation vs. insemination. In consideration of the Brown-headed Cowbird's intense insemination activity suggested here, it is notable that copulations are apparently relatively seldom observed in this species. This is true even in studies devoted particularly to cowbird mating systems and reproductive behaviors (Laskey 1950, Teather and Robertson 1986). Although cryptic timing and locations of copulations may seem a forced explanation for this, the more diffuse and broad locations of the two sexes may possibly

more handicap observation of copulation in this species in comparison with those of more limited and structurally defined territorial associations.

Site fidelity. Six of the 14 female cowbirds were recaptured at the study area for a span of from 2 to 4 years (Fig. 9, upper panel). This is consistent with a notable degree of year-to-year site fidelity previously reported in cowbird pairs (Dufty 1982). The impression that my males did not show as much site fidelity as the females (Fig. 9, lower panel) is probably an artifact of the relatively short period during which males were seen and netted each spring to early summer. If male and female captures occurring 13 May and before are compared (Fig. 9, upper vs. lower panel), then comparably 3/13 of the females and 2/10 of the males reveal year-to-year site fidelity.

NORTHERN ORIOLE

Sperm release. Males were releasing sperm from about the time of arrival in the last week of April through at least the first week in June (Fig. 10, lower panel). Cloacal spermatozoa were lacking in only four males. One of these ("C," Fig. 10, lower panel) very likely was sterile, since at none of the five times of capture and recapture did it have any cloacal sperm. All other recaptured males did. The other three spermless males were each captured and lavaged only once. Two of these were first nuptial males and one was older. Age was unlikely to be a factor in this since the ranges and distributions of lavage sperm counts were highly variable and did not notably differ between first nuptial and older males, as was true also in others of these species having distinct age-class differences in plumage (e.g., Rose-breasted Grosbeak, Indigo Bunting, and Red-winged Blackbird). The pronounced individual variation in male lavage sperm numbers (CSI 1.0 to ≈ 4.0 , = <10 to about 4.0×10^6 sperm/lavage set) throughout the season suggests that one negative record is insufficient evidence for diagnosing sterility.

Inseminations. Timing of courtship and reproduction by Northern Orioles in Colorado, well described by Edinger (1988), provides a basis for interpretation of some of my data regarding the timing of inseminations, insofar as possible populational and/or subspecific differences can be discounted. In Edinger's study: (1) males started defending territories immediately after arrival; (2) females arrived about 5 days later and were courted immediately; (3) most females started

nest building within 10 days of arrival, completed the coarse outer shell in 4 to 5 days and the lining in another 4 to 6 days; (4) most copulations (16/20) occurred during nest building; (5) egg laying and some (4/20) copulations took place during or within a day of laying; (6) pair and extra-pair copulations temporally were centered in the early morning, at about 06:00 and 07:00, respectively. In relation to times of captures of my females with and without cloacal sperm, there was no indication of differences from an essentially uniform distribution from early morning to evening and during each of the two insemination periods.

Females were seen, netted, and lavaged within the week of first hearing, netting, and lavaging of some of the resident males. Insemination of one of the females ("B," Fig. 10, upper panel) occurred 4 May, the fourth day of its presence and a week after the first detected resident female arrival. The cluster of inseminations 12 to 13 days after first female arrival is interpreted as representing the population mode for the first brood. These populational inseminations occupied a comparatively few days as compared with the span of days during which both pair and extra-pair copulations were counted by Edinger (1988) and allocated to days before and after the first layings by the females. My tentative conclusion for this species, as for some of the others, and especially the Red-winged Blackbirds, is that it may be only the relatively late copulatory acts, those near the time of laying, that are accompanied by effective insemination. A comparable cluster of inseminations 20 to 21 days later is tentatively taken to represent the start of the next brood. But this time is at the short end of the combined lengths of reported incubation (11–14 days) and nestling (11–14 days) periods for the species (Burns 1915, Harrison 1978, Edinger 1988).

Remaining thus a question is the precise temporal relationship of the insemination(s) for the second brood. The quiescent period between the two insemination periods surely represented incubation and probably the beginning of the hatchling period. But it is not clear here, nor for the other species, at what point through the nestling-fledgling transition the female is inseminated, presumably for a nearly immediately subsequent brood.

My female Northern Orioles began to show signs of beginning brood patches by 4 and 5 May,

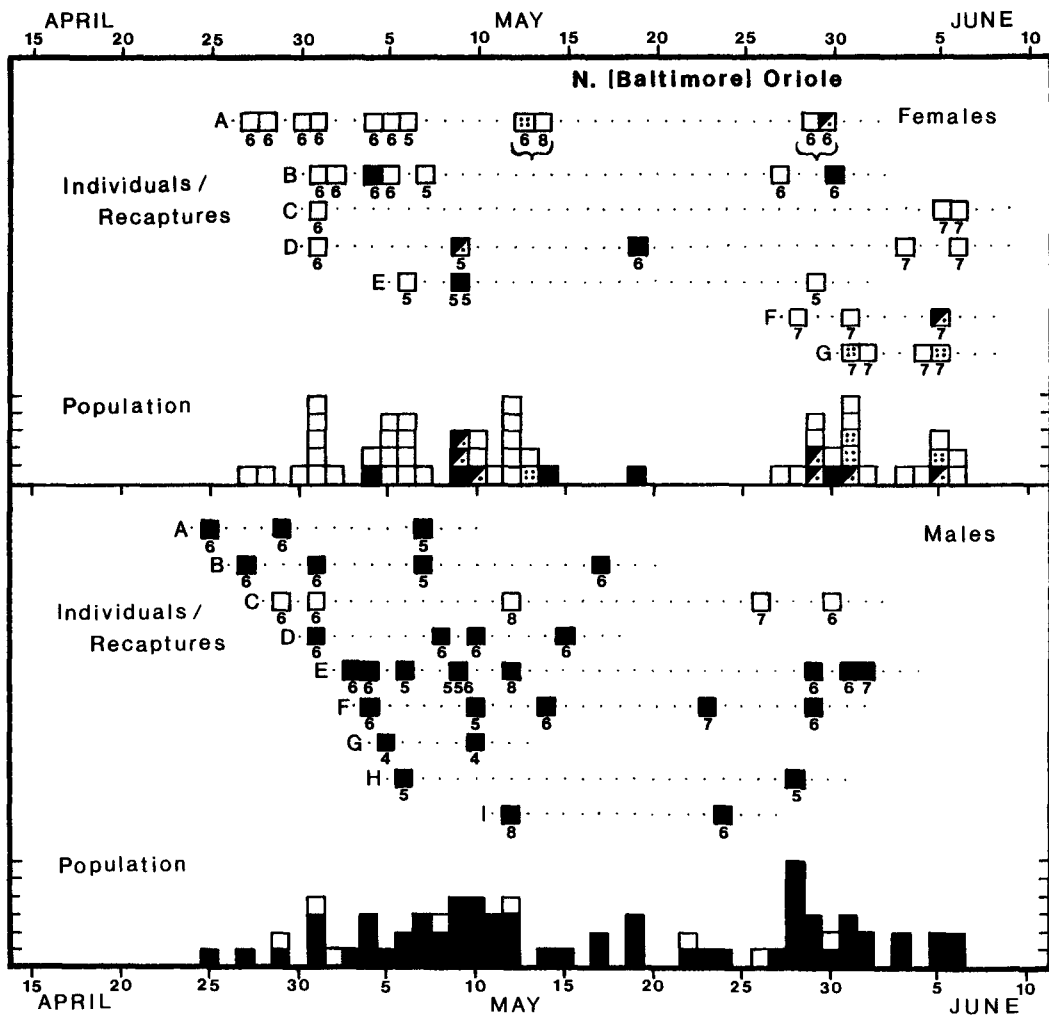


FIGURE 10. Chart of cloacal lavage sets from Northern Orioles at Foley, Missouri. Symbols, letters, and numbers are keyed as in the legend for Figure 3.

with medial thinning of breast feathers and the start of edema (code +). From 6 to 9 May, some females already had nearly full-sized patches (to 26 mm maximum diameter) with near maximal (++++) edema and moderate (+++) hyperemia. By the time of the second insemination period female brood patches were generally maximal in size and activity 32 ± 2 mm maximum diameter; edema +++++, hyperemia +++++. Also at this time (29–31 May) there were some provisionally regressive signs: flaccidity and sagging of the edema wrinkles and blisters, mild yellowing and often small petechia, and more stellate dermal blood spots. This pro-

cess was more advanced 5 to 6 June with further drying and yellowing of the brood patches.

By the time of the start of the second insemination period, female vent size and lip thickening had lessened markedly from the earlier laying and incubation during the time of the first brood. Nevertheless, by a few days into the second insemination period individual variation was prominent in female vent size and characteristics. Most were medium size (3.0 ± 0.3 mm inside transverse diameter) and thick-lipped (to 2.4 and 3.8 mm thick in the sagittal plane, anterior and posterior lips, respectively). But three had an intermediate postlaying flaccid vent, 31

May, 5 June, and 6 June. Recapture females "C" and "D" (Fig. 10, upper panel) represented this condition on the latter two dates. Although cloacal lavages apparently missed these females' inseminations and that probably occurred during the second insemination period, the large and flaccid vents indicated that laying occurred at about that time.

SUMMARY AND CONCLUSIONS

Study of contents of sperm and sperm fragments in standardized cloacal lavages from both sexes of six resident species of emberizids provides new and quantitative information about the timing of several reproductive events not previously accessible for analysis in passerine birds. Although gonadal size and weight have long been used as indicators of passerine reproductive development, they are temporally and physiologically relatively remote from actual sperm release by males and insemination of females. These reproductively critical capacities and events are immediately, quantitatively, and repeatedly assayable by cloacal lavage over either short or long periods of time in free-living populations, without harm to the individual birds.

The act of copulation has for many years been observed in passerine species. But it is inadequate as a substitute for direct, objective, and unambiguous detection and quantification of insemination by means of cloacal lavage of females. It is suggested that in at least several of the species studied here, only the copulations at or near the time of laying are accompanied by insemination. Therefore, in these passerines, as has been noted previously for example in some raptors and waterfowl (Newton 1979, McKinney et al. 1984, Robertson 1986), copulations occur in both fertilization and nonfertilization contexts and time periods.

Cloacal lavages from frequently recaptured emberizid females show that cloacal occurrences of whole sperm are brief, probably representing an early postinsemination period of a few hours or within the day of insemination. Sperm fragments in CLs from emberizid females are more irregular in their temporal occurrences but, nevertheless, can serve as indicators of a late postinsemination period. They appear to be chiefly associated with the sperm breakdown and voiding characteristic of two circumstances: release of some sperm stored or held within the female tract for several weeks, and more rapid

and temporally irregular release of sperm on a short-term basis. The first of these circumstances characterizes especially the second insemination period of monogamous emberizids and those with more structured and closely regulated insemination periods and reproductive phases (i.e., Northern Cardinal, Rose-breasted Grosbeak, Red-winged Blackbird, and Northern Oriole). The second of these circumstances characterizes particularly times of intensive and repeated inseminations when probably there is sperm excess or more rapid turnover and voiding with respect to the probable sperm-holding/storage mechanisms of the female reproductive tract. This kind of situation typified the species with more variable mating patterns, frequent inseminations, and less structured or regulated phasing of reproductive events (i.e., Indigo Bunting and Brown-headed Cowbird).

Important time points and time spans leading to and occurring within the reproductive season of these emberizids can be noted and defined in terms of the monitored changes in the sperm and sperm fragment contents of cloacal lavages. This is illustrated by Table 3, essentially a progress report summarizing features reported here, and open to revision and extension in further studies on these and other passerine species and populations. These temporal features should allow new kinds of quantitative appraisal of the effects of environmental, social, and other factors on aspects of reproductive timing, and the responses by particular members of an avian population.

Finally it is important to recognize the fact that the kinds of events and reproductive phases resolvable from cloacal lavage results for these species are not likely to be similarly detectable in most nonpasserine groups. This conclusion is based upon comparable lavage experiences with large samples from some other common avian groups, particularly those in which males have so far not shown spontaneous continuous sperm release and females seem to have a much more rapid and/or complete cloacal transit by postinsemination sperm.

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TABLE 3. Summary of species characteristics and comparisons of reproduction-related characteristics and time points as assayed here by means of cloacal lavages.

Sex and characteristic	Species ^a	Cardinalinae			Icterinae		
		NOCA	RBGR	INBU	RWBL	BHCO	BAOR
Males:							
Start sperm release:		4-7+ April	by 26 April	by 27 April	13 April	by 5 April	by 25 April
Re. m(igration)/a(rrival):		0-4 days post	some in m.	all by a.	≈9 days post	≈ at a.	all by a.
Pre 1st inseminations (days):		12-15	8+	9+	22	11+	9+
Continuity of sperm release:		except during incubation?	?	yes	yes	yes	yes
Percent males releasing sperm:		93	82	100 ^b	100 ^b	100	92
1st insemination phase:		100	92	100	100	?	93
2nd insemination phase:							
Females:							
2 insemination phases:		no	yes	yes	yes	no	yes
1st insemination phase:							
Approx. start:		19 April	4 May	6 May	5 May	17 April	4 May
Days post 1st ♀ arrival:		17 ± ?	4	6	27	12 ± ?	7
Approx. midpoint:		24 April	6-7 May	10 May	9 May	—	9 May
Percent captures with whole/fresh sperm:		29	58	13 ^c	21 ^c	59	23
Sperm fragments:		0	0	9 ^c	6 ^c	39	15
						≈(17 April-13 May)	
						≈(15 May-5 June)	
2nd insemination phase:							
Approx. start:		—	27 May	24 May	28 May	—	29 May
Approx. midpoint:		—	?	29 May	30 May	—	1-2 June
Percent captures with whole/fresh sperm:		0	25	29	10	78	29
Sperm fragments:		—	25	54	43	74	41

^a Alpha species codes, according to page addition (July 1988) to North American Bird Banding Manual; species in same order as named fully in Table 2.

^b Omitting probable transients/floaters.

^c Not omitting possible transients.

^d Not = "insemination phases", but presented as similar time periods for interspecific comparisons.

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