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CLOACAL PROTUBERANCE AND CLOACAL SPERM IN PASSERINE BIRDS: COMPARATIVE STUDY OF QUANTITATIVE RELATIONS[1]

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Abstract. Size of cloacal protuberance, a putative criterion of male sex and breeding condition in many passerines, and number of sperm in cloacal lavages were determined in males of 21 passerine species (n = 275 individuals), at Foley, Missouri, 1 to 14 May 1984. The objective was to test the quantitative relations of these two measures and to compare their vernal temporal changes. Relative size of the cloacal protuberance (cp) was scored, providing a cloacal protuberance index (CPI: 0 to ++++). Numbers of sperm in lavages without massage were estimated from counts using phase contrast microscopy of dried smears, giving a cloacal sperm index (CSI: 0 to 5.0 = 0 to 1.2×10^7 sperm/lavage). Correspondence between CPI and CSI was generally slight to lacking. Indeed, some males lacking a cp had abundant cloacal sperm, either as migrants and/or during the beginning of their breeding and nesting, while some others of the same species with a well developed large cp lacked cloacal sperm. The CSI was equivalent in first-year and older male Indigo Buntings (*Passerina cyanea*), although secondary sex, or dimorphic, characteristics (CPI and plumage) were greater in the latter. It is concluded: (1) that in examined passerines, presence of a large cp can be used as a criterion of male sex, but that its absence or small size is not a valid criterion of either sex; (2) cloacal release of normal sperm in large numbers occurs in males both with and without a cp, and therefore the cp is not a reliable criterion of breeding capability.

Key words: Cloacal protuberance; cloacal sperm; reproductive organs; breeding condition.

INTRODUCTION

The cloacal protuberance or promontory (promontorium cloacale) has been recognized for many years as a distinctive feature of many male passerine birds during the "breeding season" (Fatio 1864, Gadow and Selenka 1891). It is produced by a swelling around the posterior wall of the proctodeum and contains the seasonally expanding and convoluting, bilateral glomus seminale (also known as seminal vesicle or seminal sac) of the ductus deferens (King 1979). This terminal part of the passerine ductus deferens is believed to function in storage, maturation, and propulsion of spermatozoa (Middleton 1972, Lake 1981). The cloacal protuberance itself protrudes externally in a chiefly posterior direction and carries with it the encircled vent. Structure, variation, and taxonomic occurrence of the cloacal protuberance have been described by Drost (1938), Wolfson (1952, 1954a, 1954b) and Salt (1954), and more recently reviewed by Lake (1981) and King (1981).

In the sexing of living passerines on the basis of external characteristics, the cloacal protuberance (cp) is sometimes the only known positive criterion for the identification of males when plumage, measurements, and other features show little if any sexual dimorphism (Drost 1938, Mason 1938, Wood 1969). The variability of this "breeding" male criterion has been noted (Sheppard and Klimkiewicz 1976), but some texts still sanction its use as "an unquestionable indicator" of male sex and breeding condition (Pettingill 1970). In the resolution of this continuing problem it is necessary to take a more analytical approach. This follows from the truism that not only are maleness and breeding condition separate, although related, states, but also that each is a complex result of a number of different contributing factors.

The primary objective of the present study was to evaluate the relationship of presence and size of the cp with the occurrence and number of cloacal sperm, as a partial test of the hypothesis that presence and size of the cp are reliable criteria for male sex and breeding condition or capability respectively.

I have shown elsewhere (Quay 1984) that a cloacal lavage technique can be used to determine the presence and relative number of spontaneously released sperm. Presence of large numbers of normal sperm in a cloacal lavage from a male indicates the release of mature sperm, a component of breeding capability. Behavioral capability for breeding remains an unknown quantity without other kinds of evidence. The collection of living avian sperm by artificial means is often carried out with domesticated and captive species in relation to the needs of artificial insemination (Gee and Temple 1978). Collection of avian sperm from feral species for physiological studies was pi-

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oneered by Wolfson (1952, 1960) but since that time has been neglected.

MATERIALS AND METHODS

Birds (275 individuals, 21 species) were mist-netted at a site 5 km (air line) NNW of Foley, Lincoln County, Missouri (39°08′N and 90°46′W), 1 to 14 May 1984. For the critical evaluation of the data, especially in relation to temporal and species differences, the local status of investigated species at the time of the study is important, and is given in Table 1. Although design of the study preceded the collection of data, the particular species whose data were used depended upon retrospective selection of those that had adequate representation of both a cp and cloacal sperm, and sufficient individuals so as to be informative. These were the sole criteria for choice of species.

In most respects, birds were processed as described previously (Quay 1984, 1985a, 1985b). The relative size or mass of the cloacal protuberance (cp) was noted by means of an index system, from lacking (0) to near maximal size (+ + + + to + + + + +). The latter size category was seen in some resident and territorial males of most species. The correspondence between cp indices (CPI) and cp measurements of the studied species is provided in Table 2 for reference purposes. The scoring of CPI was used as the basis for comparisons of cp size, since I found that no single dimensional measurement of the CP had a linear, or adequate, representation of overall cp size or mass in many of the species and within all segments of the ranges in CPI. Also I have found that plots of height vs. diameter of cp are variously linear or nonlinear depending upon species and other factors (Quay, unpubl.). For Table 2 and other studies, cp height was measured vertically from one side of the base of the cp in a parasagittal plane, and diameter was measured transversely across the base of the cp. Cloacal lavages (cl) were taken by a technique described previously (Quay 1984), with some additions. Two cls were taken first from each bird without intentional stimulation or overt massage. Following this, some birds received a brief but standardized bilateral massage of the cp or cloacal region just prior to the taking of a third, and sometimes a fourth, cl.

Quantitative evaluation of the dried cls was done by phase contrast microscopy with a Leitz Laborlux 12 microscope. A cloacal sperm index (CSI) was devised based upon the approximate average number of sperm per microscopic field (10X ocular, 40X objective lens). With a standard size of lavage area on each slide, an estimate of total number of sperm per lavage could be made. Because of the great differences between species in sperm length and the difficulty of counting densely aggregated sperm, the highly refractile sperm heads were used as the objects upon which counts were based (Fig. 1). The general accuracy and consistency of the CSI technique was evaluated by means of more detailed counts of sperm within microscopic fields at intervals in a grid-like array over the entire lavage area on particular slides from different species and at dif-

TABLE 1. Species* used and their local status** at the time of study.

Hirundinidae:	
Hirundo rustica (Barn Swallow)	M + R
Paridae:	
Parus atricapillus (Black-capped Chickadee)	R: T B N I
P. bicolor (Tufted Titmouse)	R: T B N I
Muscicapidae:	
Catharus ustulatus (Swainson's Thrush)	M
Turdus migratorius (American Robin)	m + R: T B N I
Mimidae:	
Dumetella carolinensis (Gray Catbird)	M + r: T
Toxostoma rufum (Brown Thrasher)	m + R: T B N I
Emberizidae:	
Parulinae: Wood-Warblers	
Oporornis formosus (Kentucky Warbler)	M + R: T
Geothlypis trichas (Common Yellowthroat)	M + R: T
Icteria virens (Yellow-breasted Chat)	M + R: T
Thraupinae: Tanagers	
Piranga rubra (Summer Tanager)	M + R: T
P. olivacea (Scarlet Tanager)	M + R: T
Cardinalinae:	
Cardinalis cardinalis (Northern Cardinal)	R: T B N I
Pheucticus ludovicianus (Rose-breasted Grosbeak)	M + R: T
Passerina cyanea (Indigo Bunting)	M + r
Emberizinae:	
Spizella pusilla (Field Sparrow)	m + R: T B N I
Icterinae:	
Agelaius phoeniceus (Red-winged Blackbird)	m + R: T
Molothrus ater (Brown-headed Cowbird)	m + R: B
Icterus spurius (Orchard Oriole)	M + R: T B
I. galbula (Northern Oriole)	M + R: T B
Passeridae:	
Passer domesticus (House Sparrow)	R: T B N I

* Names and sequence according to the American Ornithologists' Union, (1983).

** Key to status symbols: B = breeding (behavior and/or cloacal sperm in ♀s), I = incubating (nests with eggs and/or incubation patch in ♀s), M/m = migrants (some to all/few if any), N = nesting (nest-building or use), R/r = residents (some to all/few if any), T = territorial (♂ behavior at consistent site[s]).

TABLE 2. Correspondence of cloacal protuberance index (CPI) to height (H) and diameter (D) of the cloacal protuberance in males of example species.*

	CPI					
	0	+	++	+++	++++	+++++
Species**	H D	H D	H D	H D	H D	H D
Black-capped Chickadee	1.8 × 3.1	2.5 × 3.5	3.2 × 3.9	3.8 × 4.4	4.5 × 4.8	5.1 × 5.3
Tufted Titmouse	1.4 × 3.7	3.2 × 5.2	5.1 × 6.3	7.0 × 7.6	8.9 × 8.8	10.7 × 10.1
Swainson's Thrush	2.8 × 4.0	3.7 × 5.3	4.6 × 6.6			
American Robin	3.8 × 7.2	5.3 × 8.2	6.7 × 9.1	8.1 × 10.1	9.5 × 11.1	11.0 × 12.0
Gray Catbird	3.1 × 5.1	3.7 × 6.3				
Brown Thrasher	3.2 × 5.9	4.7 × 6.4	6.2 × 7.1	7.6 × 7.9	8.8 × 9.0	9.8 × 10.2
Kentucky Warbler	2.1 × 4.1	3.6 × 4.5	4.8 × 5.0	5.9 × 5.7	6.7 × 6.5	7.2 × 7.4
Common Yellowthroat	2.1 × 2.8	2.8 × 3.2	3.5 × 3.6	4.1 × 4.1	5.1 × 5.3	
Indigo Bunting	2.2 × 4.0	3.0 × 4.6	3.9 × 5.1	4.7 × 5.6	5.5 × 6.1	6.3 × 6.8
Red-winged Blackbird	3.8 × 6.0	4.8 × 6.8	5.9 × 7.5	7.0 × 8.2	8.0 × 9.1	8.2 × 10.2
Northern Oriole	2.9 × 5.2	4.2 × 5.9	5.3 × 6.7	6.4 × 7.6	7.4 × 8.6	8.3 × 9.7
House Sparrow	1.8 × 4.3	3.1 × 5.2	4.3 × 6.2	5.5 × 7.2	6.8 × 8.2	8.0 × 9.2

* Height and diameter measurements (in mm) are median values taken from segments of plots based upon data from years 1984 and 1985 and including those from the study site; omitted studied species had relatively small numbers and/or short ranges of cp measurements for plotting.
** Names and sequence as in Table 1.

ferent times. A table of correlated values (Table 3) was obtained thereby and serves chiefly to provide mean orders of magnitude of numbers of sperm per lavage. The CSI for a particular bird at a particular sampling time was averaged from the two lavages without stimulation, to the nearest 0.5.

RESULTS AND DISCUSSION

Observations were derived from two kinds of sampling schedules: recaptures and single captures.

RECAPTURES

Data from recaptures are summarized in Table 4, and involve 17 individuals representing 11 of the 21 species. Three categories of effects or changes can be examined here:

Effects of procedures. It is primally evident that the procedures of handling and cloacal lavage were not visibly harmful to the birds (Table 4). Four of these male birds were first captured and lavaged at this site in spring 1983, and they were recaptured and relavaged on two to four occasions during the study period of 1 to 14 May 1984.

Effects of sperm removal. Removal of cloacal sperm by lavage did not markedly diminish the CSI of the particular bird when examined next, either later the same day and/or on subsequent days. For example, Cardinal #941-79171 was recaptured and lavaged twice on each of three occasions at about 12-hr intervals (Table 4); the estimated total numbers of sperm removed on each occasion (sum of the two lavages per occasion) were: 6.6×10^5, 3.0×10^6, and 4.8×10^5. Kentucky Warbler #970-86666 also was recaptured and lavaged twice on each of three occasions at approximately 6.5- and 11.5-hr intervals (Table 4), with estimated total numbers of sperm removed per occasion being: 5.5×10^6, 6.6×10^4, and 1.2×10^6.

Changes in CPI and CSI with time. CPI increased in seven, decreased in four, and was variable or indeterminate in six, of the recaptured birds (Table 4). In CSI a trend for increase with time was more apparent but still not impressive statistically; CSI increased in nine, decreased in one, and was variable or without change in seven (Table 4). In five of the nine increases in CSI the change was from no detectable cloacal sperm to presence (CSI = 1.0, $n = 1$) or to abundance (CSI = 2.0, 2.5, 3.0, 3.0, $n = 4$) in from two to seven days.

SINGLE CAPTURES

Results from single capture lavages will be presented first for those species that are represented solely or chiefly by migrants at the site and time of study, and by those sampled in greater numbers.

Swainson's Thrushes (Catharus ustulatus). Swainson's Thrushes in Missouri are known only as migrants. Sexing of individuals of this species on the basis of external features has depended upon brood patch (for nesting females only), cloacal protuberance, and wing chord (Bird Banding Offices of the United States and Canada, 1977). Since the last of these characteristics actually does not separate most birds, cloacal protuberance (cp) when present is the remaining criterion for recognizing males. The data of Table 5 demonstrate that about three quarters of early May migrants at Foley had a cp and might be considered males on this basis. However, the relative size of the cp was highly variable and showed no clear trend with time. Cloacal sperm, on the other hand, appeared only during the last four days of the sampling period and were not correlated with size of cp. In fact, they occurred in small numbers in an individual lacking any

TABLE 3. Correspondence of cloacal sperm index (CSI) with sperm numbers per microscopic field and per lavage.

CSI	Sperm/Field	Sperm/Lavage
0	0	0
1.0	0.00004	1 to 10
1.5	0.0125	1.5×10^3
2.0	0.5	6.0×10^4
2.5	2.0	2.4×10^5
3.0	5.0	6.0×10^5
3.5	12.5	1.5×10^6
4.0	33.0	4.0×10^6
4.5	67.0	8.0×10^6
5.0	100.0	1.2×10^7

sign of a cp. If one can assume that no breeding takes place during migration, this individual lacking a protuberance would have to be identified as a male.

Gray Catbirds (Dumetella carolinensis). This species at the time and site of study probably consisted chiefly of migrants (Table 1), although a few individuals appeared to be territorial; certainly some bred and nested in the vicinity within a short time. None of the captured catbirds had a brood patch at the time of sampling. Identification of sex by external features has been possible only on the basis of the presence of either a brood patch (females) or cp (males; Bird Banding Offices of the United States and Canada, 1977). Of the 44 catbirds captured, 12 lacked even a trace of a cp, but half of these had cloacal sperm (Table 6). Furthermore, many of the birds lacking cloacal sperm did have a cp (Table 6).

Indigo Buntings (Passerina cyanea). During the days of sampling for this study at least most of the Indigo Buntings were migrants (Table 1), although some probably bred and nested in the area a little later. None of the 17 females captured and lavaged during the 1 to 14 May study period had a brood patch, nor did any have cloacal sperm. The pattern of increasing numbers of males and increasing CSI during the two-week sampling period (Table 7) is consistent with the interpretation that a major migratory influx was occurring and that mean CSI was increasing.

It is possible at this season not only to distinguish male from female Indigo Buntings but also first-year males (hatched the previous year) from "adult" males on the basis of plumage color, with some or all wing (primary) coverts brown indicating first-year males, and all coverts blue indicating older ("adult") males. The validity of this criterion has been most recently reconfirmed in tests by Payne (1982). The 65 males in my sample included 36 with scattered brown feathers among the blue, following a percentage pattern in the dorsal plumage as a whole similar to that of the wing coverts. Although there was no significant difference in

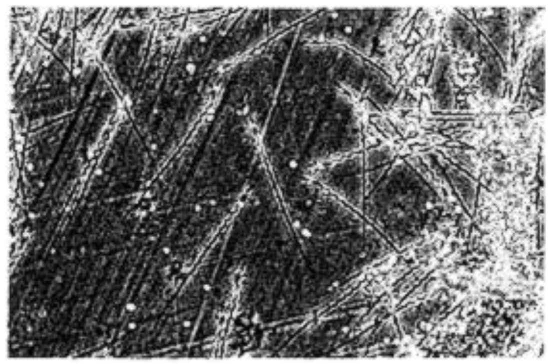

FIGURE 1. Photomicrograph of a typical non-stained cloacal lavage specimen under phase contrast (×400). Male American Robin with a CSI of 4.0. (Kodak Tri-X Pan film).

CSI between parti-colored (first-year) and unicolored blue (older) males, there was a trend for greater extent of blue plumage in birds with a more distinct and prominent cp (greater CPI, Fig. 2). This was most distinct when the birds were segregated according to having ≥95% of the plumage blue in contrast to those having a lower percent of the plumage blue (or ≥5% brown). A Chi-square test for differences in probabilities (Conover 1980) was applied to the data of a $R \times C$ contingency table derived from the matrix of Figure 2, and in which eight columns corresponded to the eight steps in the CPI and the two rows corresponded to the two age classes based upon 100% blue plumage = "adult" (older) and some brown feathers among the blue = first-year males. The probability of the two age classes having equivalent distributions of CPI was <0.02, confirming the different trends noted above and depicted in Figure 2. However, the two age classes were not significantly different in either means or distributions of CSI.

In male Indigo Buntings, as in the sexually indeterminate Swainson's Thrushes and Gray Catbirds, CSI and CPI appeared to have weak (if any) ties (Fig. 2). For example, three of the five males lacking a cp had abundant cloacal sperm, and three of the five males lacking cloacal sperm had a large cp (Fig. 2).

Other species. Data representing the remaining eighteen species are given in Table 8. It is seen here again that in those species for which a cp is the only external criterion of maleness, cloacal sperm can be abundant in individuals lacking a cp (Tufted Titmouse, *Parus bicolor* and Brown Thrasher, *Toxostoma rufum,* bracketed data). These individuals also lacked a brood patch, although other individuals in the population had a brood patch but neither cp nor cloacal sperm. In the other sixteen species, those in which males could be identified by other characteristics, cloacal

TABLE 4. Changes in CPI* and CSI* with time in 17 recaptured males of 11 species.

Species FSW Band #**	Date (May 1984) 2	3	4	5	6
Tufted Titmouse					
1321–23193***			+++/0		
Swainson's Thrush					
1331-16152		?/0			
16154		+++/0	++/0		
Kentucky Warbler			time: 0630 1300 0630		
970-86666***			+/4.0 ++/2.5 ++/3.0		
Common Yellowthroat					
1650-48049***		?/2.0			
Summer Tanager					
941-79151***					
Northern Cardinal			time: 0630 1800 0630		
941-79171	0/1.5		+/2.5 +/3.5 0/2.5		
Indigo Bunting					
970-86705					+/2.0
86712					
Field Sparrow					
970-86681		++/2.0			
Brown-headed Cowbird					
821-20414					0 – +/0
941-79172	?/0		++/1.0		
79182		0/0			+/0
79196			?/1.0		
Northern Oriole					
821-20403				+/3.0	
House Sparrow					
1331-16142	++/0.5		?/0		
16148	+++/2.0				+++/2.0

* Cloacal protuberance index (CPI) and cloacal sperm index (CSI) are given as CPI/CSI with values of 0 to +++ and 0 to 4.5 respectively; ? = values not known.
** FSW Band # = permanent band number of the U.S. Fish & Wildlife Service.
*** These individuals were first banded and lavaged at this site and this season in 1983.

sperm often occurred in individuals lacking a cp. Near the other end of the range in CPI there were several individuals that lacked sperm in the two lavages taken without, or prior to, cloacal massage. Brief bilateral massage of the cloacal region produced sperm in cloacal lavages of these individuals representing three different species (Table 8). This suggests that negative evidence consisting of no sperm in lavages without stimulation is not a reliable indication of lack of sperm in the glomus seminale or terminal part of the ductus deferens. In the present study comparatively few birds received a cloacal massage, but those that did following two lavages containing sperm, often gave a postmassage lavage with a slightly higher CSI.

SIGNIFICANCE OF THE CLOACAL PROTUBERANCE

Critique of the CPI. Relative size of the cp was evaluated in this study chiefly through the use of an arbitrary index or scale similar to, but more detailed than, those often employed in

TABLE 5. Distribution of cloacal protuberance and cloacal sperm indices* in relation to date (1 to 14 May) in migrating Swainson's Thrushes.

Cloacal Protuberance Index	Date: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Σ
+++			00	000											5
++ to +++													0		1
++**		0	0	0	0	0			0		00?		00	X (3.0)	12
+ to ++										0	X (3.0)	0		0	4
+			0		0					00	00	0			7
0 to +								0	0	0					3
0				0	0					0	?0??	00X (1.0)			10
Σ		1	4	5	3	1	0	1	2	5	10	5	3	2	42

* Cloacal sperm index = 0, except in cases marked by X (index in parentheses) or by ? (no lavage taken).
** Mean diameter of cloacal protuberance at base = 5.6 mm.

TABLE 4. Extended.

Date (May 1984)							
7	8	9	10	11	12	13	14
				+/3.0			
				+ − ++/3.0			
			+++/3.0				
			+/3.5				
					+/2.5		0/3.0
			++ − +++/4.0				
0 − +/2.0					++/2.0		
				+++/2.0			
			+ − ++/2.5				
+ − ++/2.0							
						0 − +/1.0	
			++/3.0				
+ − ++/4.5							
					++/1.0	+++/2.5	

* Cloacal protuberance index (CPI) and cloacal sperm index (CSI) are given as CPI/CSI with values of 0 to +++ and 0 to 4.5 respectively; ? = values not known.
** FWS Band # = permanent band number of the U.S. Fish & Wildlife Service.
*** These individuals were first banded and lavaged at this site and this season in 1983.

data files for banded birds. A CPI of ++ or greater in the present study corresponds to a grossly recognizable cp in the species examined. Lower CPIs (0 to +, + and + to ++), especially at the lower end, are probably marginally if at all recognized as cps by banders. No system of measurements for the passerine cp is currently recognized. There are several probable reasons for this: (1) the vent is usually surrounded by a circlet of feathers that hinders measurement of the cp. (2) The cp varies in shape, bulbous and cylindrical shapes being most commonly noted as characterizing particular species (Salt 1954). (3) Consistent measurements of height, especially, and of diameter are difficult to obtain because of some short-term variable movement or extrusion of the region by muscular or other actions by the bird. All of the CPI measurements in the present study were done before the cloacal lavage, since the latter sometimes caused a slight distention of the region through retention of fluid

TABLE 6. Relation of cloacal protuberance to cloacal sperm index in Gray Catbirds.*

	Cloacal Protuberance Index							
Cloacal Sperm Index	0	0 to +	+	+ to ++	++	++ to +++	+++	Σ
4.5					1			1
4.0			1					1
3.5			1		1			2
3.0	3		2		1		1	7
2.5			2				1	3
2.0	1				2			3
1.5								0
1.0			1					1
0.5	2	1	1					4
0.0	6	8	3	1	3		1	22
Σ	12	9	11	1	8	0	3	44

* Numbers of individuals with each combination of CPI and CSI; sexes not distinguishable.

TABLE 7. Numbers of male Indigo Buntings in relation to their cloacal sperm index and date of capture (1 to 14 May).

Cloacal Sperm Index	Date: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Σ
4.0										2	2		1		5
3.5							1	1		1	3				6
3.0									1	1	3	4	7	2	18
2.5				1	1					1	2	2	3	1	11
2.0		1				1	3	1	1			1			8
1.5		1	2		1			1		1	1	1	1	2	11
1.0					1							1			2
0.0										1	3			1	5
Σ =	0	2	2	1	3	1	4	3	2	7	14	9	12	6	66
Net hours/day*	4.4	162	249	294	294	296	321	322	332	354	364	364	337	60	
Birds/100 net hr.	0**	1.2	0.8	0.3	1.0	0.3	1.2	0.9	0.6	2.0	3.8	2.5	3.6	10.0*	
Mean sperm index***	—	1.8	1.5	2.5	1.7	2.0	2.1	2.2	2.5	2.7	2.4	2.4	2.8	1.9	

* Net hours/day = sum of hours of operation of each mist-net on that day within dawn to dusk interval.
** The limiting of net operations to late on 1 May and early on 14 May biases these values.
*** Mean sperm index = mean of cloacal sperm indices of the individuals in the column above.

by the cloaca and confluent passages. The presence or absence of accumulated fecal material also sometimes affected the degree of distension of the cloacal region. In this instance, the flushing by cloacal lavage tended to decrease slightly the distension of the cloacal region. I found that in spite of short-term changes, the CPI of a bird was reproducible plus or minus one step in the CPI scale.

Tissue and hormonal factors. It is often either stated (Bailey 1953) or implied that the contained glomus seminale on each side posteriorly is responsible for the distension of the passerine cp. Although glomal swelling contributes to the cp, cloacal and other contained or adjacent tissues participate as well. Investigations have not yet been reported concerning the possible contributions of tissue edema or of vascular-erectile mechanisms.

Work by Riddle (1927), Witschi (1945), Bailey (1953), Hilton (1968) and others has shown that growth of the passerine glomus seminale is primarily under androgenic hormonal control. Although contributions by increased content of seminal fluid and poorly defined mechanical factors are sometimes invoked

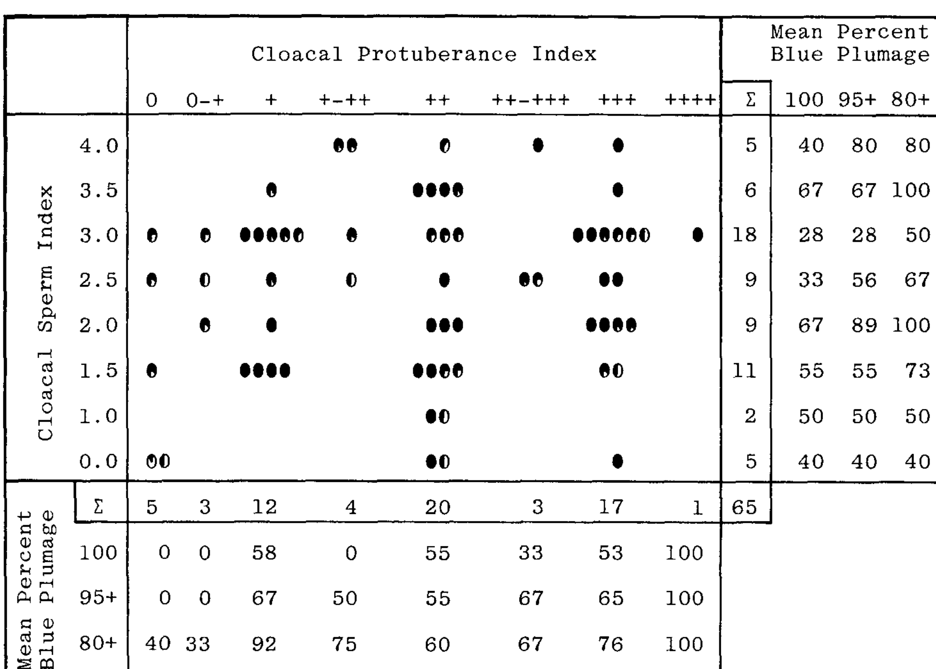

FIGURE 2. Interrelations of cloacal protuberance index, cloacal sperm index and percent blue-indigo plumage in male Indigo Buntings. Each dot in the matrix represents one bird; the extent of blackening of the dot represents the extent of blue feathers in the wing coverts and other dorsal plumage, in comparison with brown (= clear space in dot).

TABLE 8. Relation of cloacal protuberance to cloacal sperm index in males* of 18 species.

	Cloacal Protuberance Index									
Species**	0	0 to +	+	+ to ++	++	++ to +++	+++	+++ to ++++	++++	Σ
Barn Swallow			2.0		0					2
Black-capped Chickadee			0, 0 2.5		0		1.0			5
Tufted Titmouse*	[2.5]		0 3.0				0			3
American Robin	3.0						1.0		0[a] 3.5	4
Brown Thrasher*	[0, 2.5 2.5]	1.0			3.5		2.5, 3.5 4.0			5
Kentucky Warbler		0 1.5	2.5 4.0[s]		2.5[s]		3.0 3.0[s]			7
Common Yellowthroat	0		0 3.5		2.0 3.0		2.0			6
Yellow-breasted Chat	0 4.0		0 0	 3.0						5
Summer Tanager	0, 0, 0 0, 1.5 3.0		2.0 2.5 2.5							9
Scarlet Tanager	0 2.0	0	2.0							4
Northern Cardinal	0, 0 2.5, 3.0 3.5	2.0	0, 2.5 3.5							9
Rose-breasted Grosbeak	2.5 3.0						0[b], 2.5 2.5			5
Field Sparrow					2.0		2.0, 3.0 3.5, 3.5	2.0	0, 1.0, 1.0 1.5, 1.5 2.5, 3.5	13
Red-winged Blackbird				3.5	2.0 3.0		2.0, 3.0 3.0, 4.5			7
Brown-headed Cowbird	0, 1.0 3.0	0 1.0	0	2.0 2.5	1.0					9
Orchard Oriole	0 1.0	3.0	3.0 4.0				 2.5			6
Northern Oriole	0, 1.5 2.0		3.0 4.0		 3.0					6
House Sparrow	3.0	1.0	4.5	2.5 4.5	1.0 1.0 2.0		1.0, 1.5 2.0, 2.5 5.0, 5.0		0[c]	15

* Identification of sex by color and/or measurement(s) except as noted (*—sex by cloacal protuberance).
** Sequence and names as in Table 1.
[a] Cloacal massage produced CSI of 1.0.
[b] Cloacal massage produced CSI of 1.5.
[c] Cloacal massage produced CSI of 2.0.
[s] Denotes a single bird with multiple recaptures.

(Witschi 1945, Wolfson 1954a), early observations by Riddle (1927) on feral passerines with unilateral testicular atrophy support the primacy of hormonal control.

Relation to "breeding condition." Our frequent finding of cloacal sperm contents of normal appearance in spring male passerines lacking any sign of a cp weakens justification for using the cp as a major criterion of male "breeding condition." Although it has been suggested that the cp may mechanically aid in the juxtaposition of male and female vents at copulation, there is no direct evidence for improved breeding success or fertility specifically through the presence of a cloacal protuberance. Certainly many birds copulate successfully and are fertile without either a cp or an analogous intromittent device. The relations of the passerine cp to sperm production and release parallel those of various other avian secondary sexual characteristics to semen or sperm production. A lesson may be taken from the abundantly documented experience of poultry breeders in their quest for external criteria of fertility and good breeding potential in cocks: "Testis size was found to be rather highly correlated with semen production, but neither comb nor wattle size showed a significant correlation with semen production. Neither general outward appearances, nor the show of sexual activity, nor the lack of a show of sexual activity are necessarily related to semen production" (Burrows and Titus 1939).

CLOACAL SPERM: NEEDS AND CONCLUSIONS

Quantitative, physiological, and seasonal studies of sperm or semen production in passerine birds are amazingly deficient in comparison to those conducted with domestic fowl with regard to gaining information on factors affecting fertility. Quantitative studies of passerine sperm, of their production and their transport, storage, and dynamics within both male and female reproductive tracts are important but neglected areas of feral avian reproductive biology.

The present study demonstrates that: (1) Cloacal sperm samples can be easily, harmlessly, and repeatedly obtained from small passerines for quantitative study. This is a confirmation and extension of Wolfson's (1952, 1960) pioneering observations and suggestions. (2) Morphologically normal cloacal sperm can be found in spring-migratory males of some species while geographically distant from their known "breeding territories," as described previously (Quay 1985a) and as demonstrated here for the first time in Swainson's Thrushes in Missouri. (3) Large numbers of normal cloacal sperm are found in males both with and without a cloacal protuberance, both in migrants and in resident species in different phases of the beginning of their annual breeding-nesting season. (4) Numbers of cloacal sperm can be equivalent in first-year and older males of some species, although secondary sex or dimorphic characteristics may be consistently more prominent in the latter, as, for example, in the Indigo Bunting.

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