TABLE 1. Predation on natural Eurasian Black-Grouse nests and on dummy nests exposed in the same period. Numbers of nests are given in parentheses.

	1984	1985	1986	1987
Natural nests	50% (16)	46% (13)	47% (15)	47% (19)
Dummy nests	12% (50)	12% (50)	46% (50)	52% (25)

ford 1972, Sugden and Beyersbergen 1986, Storaas 1988). We found, however, that natural nests, exposed during the same period as dummy nests, were robbed mainly by mammalian predators. We speculate that these are probably attracted by the scent of the sitting hen or by her trails because she usually walks off the nest (pers. obs.). Mammals may fail to detect dummy nests that lack the scent of a hen (Storaas 1988) or may avoid dummy nests because they initially smell of humans (Fjeld and Sonerud 1984).

We do not know why predation on dummy nests increased in 1986, but corvids may have learned to search for dummy nests (Picozzi 1975). The predation rate on natural nests did not change. We conclude that predation on dummy nests is a poor index of predation on natural nests of Eurasian Black-Grouse and probably overestimates the importance of bird predation.

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Uterovaginal Sperm-storage Glands in Sixteen Species with Comments on Morphological Differences

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Sperm-storage glands (SSGs) in the uterovaginal junction (UVJ) of the oviduct play an essential role in reproduction in domestic bird species (Bobr et al. 1964a, b; Van Krey et al. 1967). Sperm that is introduced to the female's reproductive tract is stored in SSGs, and then released and transported to the infundibulum, where fertilization takes place (Lake 1975). Discovery of SSGs in several wild species has led to consider speculation regarding their significance (e.g. clutch size, mating systems; see Lake 1975, Cheng et al. 1983, Davies 1983, Hatch 1983, Fitch and

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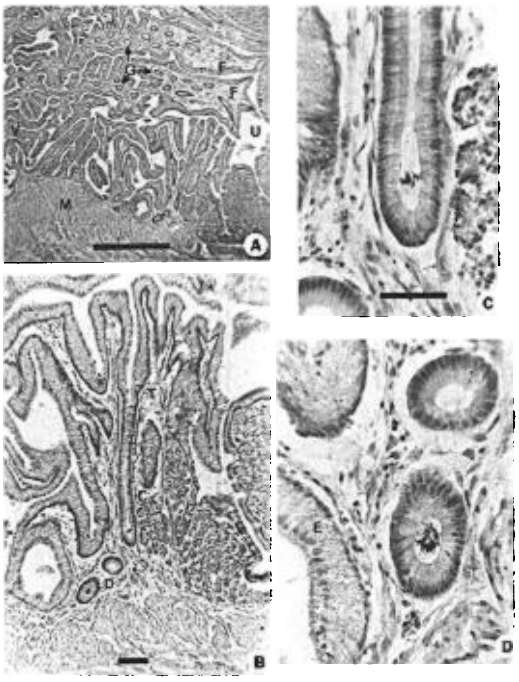

Fig. 1. (A) Longitudinal cross-section of uterovaginal junction from a Tree Swallow showing limited distribution of sperm-storage glands (G). This overview illustrates the muscular "sphincter" (M), uterus (U), and vagina (V). Bar = 1 mm. (B) Longitudinal cross-section of sperm-storage gland with sperm in distal end. Illustrated is the transition (T) from epithelium, with basal and apical cell nuclei, to a sperm-storage gland with characteristic basal nuclei. This section was 3 slices (24 μ) after the section in Fig. 1A where gland appears in bottom right. C and D refer to respective figures. Bar = 100 μm. (C) Tip of gland in 1B confirming presence of sperm. Bar = 50 μm. (D) Sperm-storage gland in cross-section illustrating typical ringlet appearance. The two cross-sections were actually one gland with a bend near the distal end. The lumen of one cross-section is filled with sperm. Epithelium (E) with alternating basal and apical nuclei is illustrated. Same scale as 1C.

Shugart 1984, Bakst and Bird 1987). The basis for discussion of SSGs and sperm storage is tenuous because it is not known if SSGs are common in avian species. Second, empirical evidence used for speculation is derived largely from studies of domestic species, which may have undergone considerable artificial selection to enhance sperm-storage capabilities. Therefore, these studies have unknown applicability to wild species (Lake 1975, Bakst and Bird 1987). I surveyed 16 wild species to determine if SSGs are present and if sperm is stored. This provides an expanded basis for discussion of the role of SSGs.

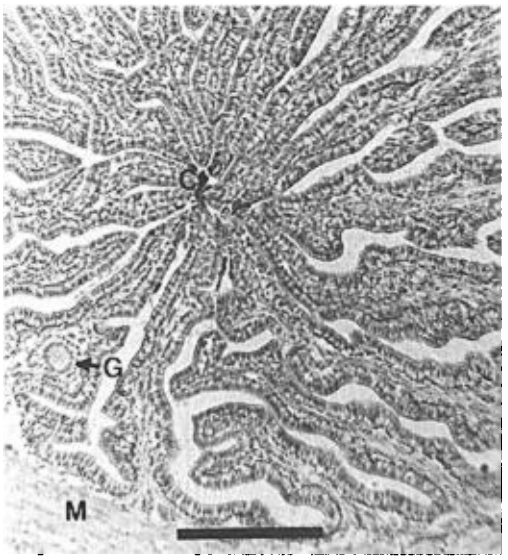

Fig. 2. Cross-section of Northern Waterthrush vagina showing folds that meet in the center (C), muscle (M) of oviduct wall, and one sperm-storage gland (G). Section is taken just before uterovaginal junction. Bar = 1 mm.

Terminology.—Sperm-storage sites in the uterovaginal region of the avian oviduct have been referred to as uterovaginal glands (Bobr et al. 1964a, Van Krey et al. 1967), sperm-host glands (Gilbert et al. 1968), sperm-storage tubules (Mero and Ogasawara 1970), and SSGs (Burke et al. 1972). There is no standard terminology in recent usage. I favor SSGs in reference to function (sperm-storage) and probable derivation (gland) (see Gilbert et al. 1968).

I examined the uterovaginal junction in specimens of the Ring-billed Gull (*Larus delawarensis*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Tree Swallow (*Tachycineta bicolor*), Veery (*Catharus fuscescens*), Cedar Waxwing (*Bombycilla cedrorum*), European Starling (*Sturnus vulgaris*), Yellow-rumped Warbler (*Dendroica coronata*), American Redstart (*Setophaga ruticilla*), Northern Waterthrush (*Seiurus noveboracensis*), Indigo Bunting (*Passerina cyanea*), White-crowned Sparrow (*Zonotrichia leucophrys*), Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle (*Quiscalus quiscula*), Northern Oriole (*Icterus galbula*), American Goldfinch (*Carduelis tristis*), and House Sparrow (*Passer domesticus*).

Multiple specimens of 4 species (Ring-billed Gull, Tree Swallow, Cedar Waxwing, Red-winged Blackbird) were collected from or near nests during the egg-laying period. Single individuals of the remaining 12 species were collected opportunistically. I obtained appropriate federal and state (Washington, Michigan) permits for collections.

TABLE 1. Quantitative summary of sperm-storage glands (SSGs) in individual specimens. Only specimens that contained sperm are listed.

Species	No. of SSGs measured	Length (μm) $\bar{x}$	Length (μm) SE	Width (μm) $\bar{x}$	Width (μm) SE	Condition[a]	% of sample SSGs empty/partially full/full
Ring-billed Gull	20	170	10	49	2	Laying (US)	20/10/70
Ring-billed Gull	20	170	9	46	2	Laying (U)	15/10/75
Ring-billed Gull	13	141	10	44	2	Laying (US)	0/38/62
Tree Swallow	9	478	30	74	4	Laying (I)	55/45/0
Tree Swallow	16	404	22	62	3	Laying (M)	63/31/07
Tree Swallow	20	524	16	64	2	Laying (US)	55/35/10
Tree Swallow	25	494	17	55	1	Laying (I)	24/72/4
Cedar Waxwing	25	99	4	49	2	Postlaying	20/72/8
Cedar Waxwing	25	126	7	57	2	Laying (U)	0/64/36
Cedar Waxwing	15	186	7	52	2	Postlaying	67/33/0
Yellow-rumped Warbler[b]	3	480	25	41[c]	1	Laying (U)	0/0/100
American Redstart[b]	2	450	10	41[d]	2	Laying (US)	0/0/100
Northern Waterthrush[b]	14	296	26	81	5	Laying (M)	0/100/0
Indigo Bunting	12	356	22	45	3	Postlaying	17/67/17
White-crowned Sparrow[b]	17	398	12	66	2	Laying (US)	6/0/94
Red-winged Blackbird	19	272	28	69	2	Laying (US)	11/11/78
Red-winged Blackbird	23	286	28	68	3	Laying (OO)	0/39/61
Red-winged Blackbird	17	233	9	69	3	Laying (I)	12/82/6
Common Grackle	18	168	16	47	1	Laying (IU)	0/12/88
American Goldfinch	22	433	15	80	4	Postlaying	77/23/0
House Sparrow	21	240	8	58	2	Prelaying	0/100/0

[a] Location of ovum/egg in the oviduct is indicated in parentheses. I = infundibulum, M = magnum, IU = isthmus-anterior uterus, U = uterus—unshelled, US = uterus—shelled, OO = between oviposition-ovulation.

[b] Specimen placed in unbuffered formalin.

[c] $n = 19$.

[d] $n = 20$.

Within 1 h of death the oviduct and ovary (for reference) were removed and fixed in 10% neutral phosphate-buffered formalin (see Table 1 for exceptions). Before mounting for sectioning, connective tissue was teased from the oviduct. In larger specimens (e.g. gulls) a 10-mm (longitudinal) slice of the uterovaginal junction was sectioned. In smaller specimens (e.g. warblers) the entire region of the oviduct was sectioned. Sections typically contained uterine, UVJ, and vaginal tissue in sequence. I also examined sections of the uterus-isthmus junction and medial vagina for comparisons.

I was primarily interested in obtaining serial sections to trace entire SSGs to determine length, three-

TABLE 2. Morphology of sperm-storage glands.[a] The percentage of the total number of SSGs is indicated.

Species (no. of birds)	Total SSGs	Tubule		Bud	
		Single	Branched	Single	Sequential
Ring-billed Gull (3)	53	81	19	0	0
Tree Swallow (4)	70	100	0	0	0
Cedar Waxwing (3)	65	0	0	97	3
Yellow-rumped Warbler (1)	3	67	33	0	0
American Redstart (1)	2	100	0	0	0
Northern Waterthrush (1)	14	21	0	0	79
Indigo Bunting (1)	12	100	0	0	0
White-crowned Sparrow (1)	17	100	0	0	0
Red-winged Blackbird (3)	59	10	30	38	22
Common Grackle (1)	18	94	6	0	0
American Goldfinch (1)	22	95	5	0	0
House Sparrow (1)	21	100	0	0	0

[a] See Figs. 1B and 3A–B for characterization of a straight tubule, Fig. 4 for a bud, and Fig. 5A–B for a sequential bud. A tubule lacks a constriction in the lumen of the gland; a bud has a severe constriction in the lumen that opens into a larger chamber.

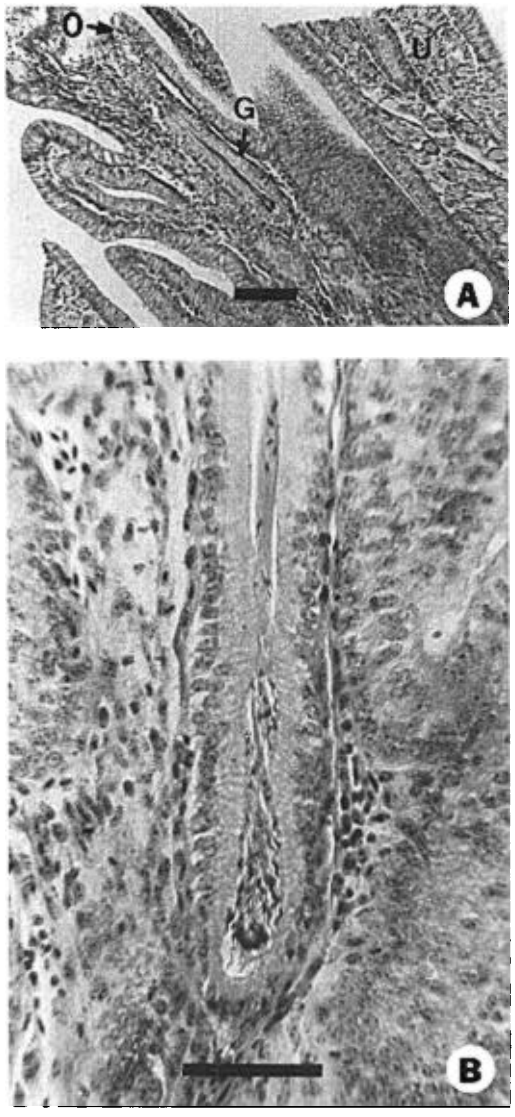

Fig. 3. (A) White-crowned Sparrow fold showing sperm-storage gland (G) in cross-section. Gland opened (O) to the lumen in previous sections. This fold was on anterior side of uterovaginal "sphincter" muscle and protruded into uterine (U) tissue. Bar = 100 μm. (B) Enlargement of 3A showing gland packed with sperm. Bar = 50 μm.

dimensional shape, and sperm load. Serial sections were made on a cryostat and stained with haematoxylon and eosin (Thompson 1966). To obtain serial sections of friable tissue, such as oviduct, I infiltrated the tissue with 30% phosphate-buffered sucrose, embedded the tissue in a solution of 5-ml Tissuetech + 1 drop 95% EtOH, and sectioned at 8 μm. Further specifics of this procedure are available on request.

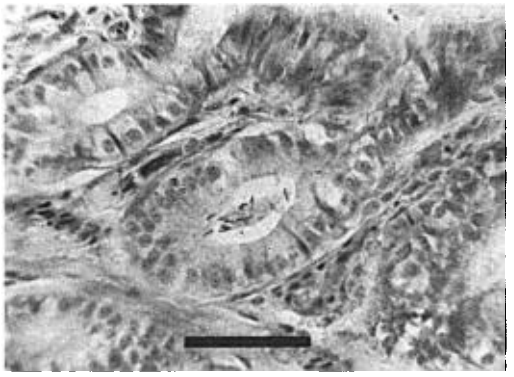

Fig. 4. Single bud-shaped gland containing sperm in Cedar Waxwing. Bar = 50 μm.

For quantification for each specimen, I used the first 25 SSGs or all those I could trace in their entirety. Therefore, the samples are unbiased. Outside dimensions were measured using a stage-calibrated ocular micrometer. For each gland measured, I ranked the sperm load as empty, partially full, or full.

Data were analyzed using the procedures and recommendations in the SYSTAT statistical package (Wilkinson 1986). I used a nested ANOVA to partition variation within and among species. The algorithm in SYSTAT adjusts for unequal subgroup sizes (Wilkinson 1986). A modification of the Student-Neuman-Keuls multiple-range tests, which adjusts for unequal group sizes, was used to identify differences among groups (Zar 1974).

The UVJ in the fixed tissue was evident as the anterior end of a "U" (inverted "S"; Bobr et al. 1964b) shaped undulation of the vagina where it merged with the uterus. In most specimens there was a darkened or denser band 2–5 mm wide (longitudinally) in the oviduct wall. This constriction appeared as a thickening of muscle (Fig. 1A), which may function as a sphincter (Bobr et al. 1964b, Gilbert et al. 1968, Gilbert 1979).

The vaginal and uterine lumen are packed with longitudinal ridges or folds (Fig. 2). The SSGs are found in these mucosal folds. Regional differences in folds (see Bobr et al. 1964b, Gilbert et al. 1968) were evident in all specimens (see Fig. 1A).

SSGs occurred in 15 of 16 species (8 of 9 families). SSGs were identified by the characteristic columnar or cuboidal cells with basal nuclei, a lumen, presence of sperm, and three-dimensional shape as determined by examining serial sections (Fig. 1A–D). Examination of uterine and vaginal folds on either side of the UVJ indicated SSGs were localized in a narrow band (Fig. 1A). No structures similar to sperm-storage glands were present in medial vaginal or anterior uterine sections examined for comparison.

Of the 15 species with SSGs, 12 (8 families) contained sperm (Table 1). Individuals of these 12 species had enlarged ovaries and oviducts, and most were laying eggs (Table 1).

SSGs without sperm were evident in 3 postlaying specimens with regressed reproductive tracts (Veery, European Starling, and Northern Oriole). These were postlaying as determined by the presence of collapsed follicles and a brood patch (see Pyle et al. 1987).

SSGs were not present or were undifferentiated in an adult-plumage Yellow-bellied Sapsucker. I collected this female and an adult male while the pair was excavating a nesting hole. The behavior and the unenlarged reproductive tract indicate the bird was in a prebreeding state. Glands may not be evident in this state, and further work is needed to determine if Piciformes and Picidae have SSGs.

SSGs had two basic shapes (Table 2). The first was the typical straight-walled tubule with a gradual enlargement near the distal end (Figs. 1B–D and 3A–B). A second shape, found in Cedar Waxwings, was a much shorter "bud" shaped structure (Fig. 4, Table 2).

A modification of the bud shape was a third form, sequential buds (Fig. 5A–B). Examination of sequential buds in serial sections indicated that distal buds appeared to empty into the previous bud through the constricted neck. This structure was confirmed by careful examination of serial sections.

SSG length was the most variable dimension (Table 1). In four species for which I had multiple specimens, SSG length differed significantly ($F = 49.9$, df = 3, 9, $P < 0.001$). There were also significant differences among individuals within some of the species ($F = 5.0$, df = 9, 230, $P < 0.001$). Multiple comparisons using group means indicated that the mean (±SE) lengths of SSGs in Cedar Waxwings (130 ± 5 μm) and Ring-billed gulls (167 ± 5 μm) were not significantly different ($P < 0.001$). Red-winged Blackbirds (266 ± 15 μm) and Tree Swallows (480 ± 11 μm) differed from one another and from the previous two species.

A number of factors might influence the size of SSGs. One is body size. For the four species considered above, overall body size was eliminated as an important influence. The Ring-billed Gull and Cedar Waxwing had relatively short SSGs of similar length but mean body masses of 515 and 35 g, respectively. The smallest individuals, the Tree Swallows (21.5 g), had the longest glands. Red-winged Blackbirds were intermediate in SSG length and body mass (46 g).

Previous studies of SSGs recorded sperm in only 2 of 4 wild species examined. This raises the question, do all species with SSG-like structures store sperm (Hatch 1983, Bakst and Bird 1987)? The presence of sperm in SSGs in all 12 species that contained enlarged oviducts and ovaries indicates that in general, wild species can store sperm.

The significance of the differences in SSG morphology is unknown. The differences may be important mechanical aspects of reproduction in wild avian species. Eventually, differences in SSGs or sperm storage may be linked to species differences in behavior (see Lake 1975, Hatch 1983, Bakst and Bird 1987). Interspecific differences may be manifestations of biological adaptations in females that affect sperm competition or the behavioral consequences of sperm competition (males' reproductive strategies) (Cheng et al. 1983, Fitch and Shugart 1984, Parker 1984). Intraspecific differences may be indicative of female physiological condition or quality (Bobr et al. 1964b, Bakst and Bird 1987).

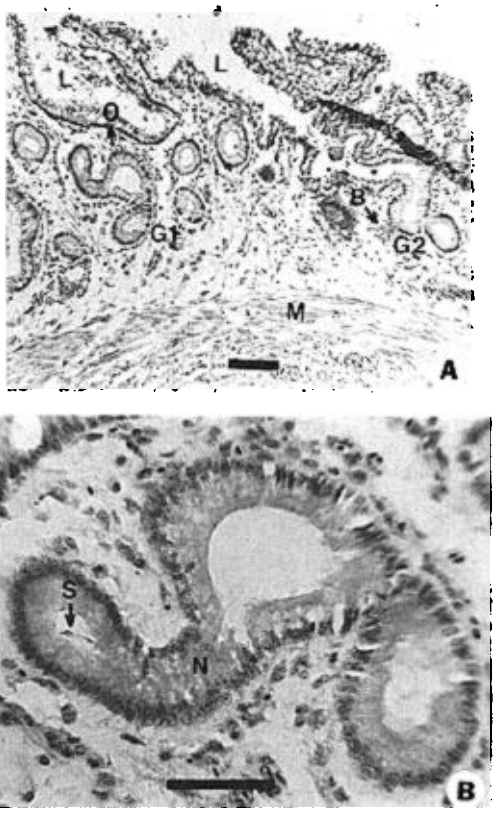

Fig. 5. (A) Cross-section of one uterovaginal fold in Northern Waterthrush. Two sperm-storage glands (G1, G2) consist of a main chamber with two buds. The base (B) of the second bud in G2 was in this section. The main chamber of G1 opened (O) to the oviduct lumen (L) three sections previously approximately at the arrow. M = muscle. Bar = 100 μm. (B) Enlargement of G1 illustrating that the neck (N) of a distal bud is not formed by a bend in a straight tube. Sperm (S) in lumen of distal bud. Bar = 50 μm.

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Effects of Food-handling Time on Scanning Rates among American Goldfinches

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Vigilance rates among foraging birds may be influenced by a number of factors, including flock size, predation risk, and energetic demands (Pulliam et al. 1982, Lendrem 1983, Metcalfe and Furness 1984, Popp 1986). One recent hypothesis predicts that scanning rates should also be constrained by the time required to handle food items (Lendrem 1983). The more time required to manipulate food items, the less time available for scanning. I investigated how food-handling times affected scanning rates among American Goldfinches (*Carduelis tristis*) foraging at a winter feeding station.

American Goldfinches were videotaped while on a feeder at Elkhart Lake, Sheboygan Co., Wisconsin, during February and March 1985. The feeder was stocked with small, black oil-type sunflower seeds (*Helianthus annuus*) or with niger (thistle) seeds (*Guizotia abyssinica*). Handling of niger seeds (typical size: 1 × 5 mm) involved simply pecking at the seeds and swallowing them. In contrast, the unhusked sunflower seeds (typical size: 6 × 12 mm) required considerable manipulation to find the crack in the husk and break it open. Handling times for the niger seed were difficult to measure but were typically around 0.1 s or faster. Handling times for the sunflower seeds generally exceeded 0.4 s (Table 1). The mean value given