MECHANISM AND ECOLOGICAL SIGNIFICANCE OF SPERM STORAGE IN THE NORTHERN FULMAR WITH REFERENCE TO ITS OCCURRENCE IN OTHER BIRDS

SCOTT A. HATCH

Museum of Vertebrate Zoology, University of California, Berkeley, California 94720 USA and U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503 USA[1]

ABSTRACT.—Sperm-storage glands were found in the uterovaginal (UV) region of the oviduct in Northern Fulmars (*Fulmarus glacialis*), Horned Puffins (*Fratercula corniculata*), and Leach's Storm-Petrels (*Oceanodroma leucorhoa*) collected before or shortly after egg laying. Previously described only in domestic Galliformes, UV sperm-storage glands may prove to be a common feature of the avian reproductive system. There is as yet no compelling explanation of their function in the Horned Puffin. In the Northern Fulmar, and probably in other petrels, however, sperm-storage glands allow the separation of the male and female over pelagic waters for several weeks immediately before egg laying. The likelihood of prolonged viability of sperm in the female reproductive tract should be considered in interpreting the sexual behavior of other wild birds. *Received 27 August 1982, accepted 18 January 1983.*

AVIAN spermatozoa survive in the female reproductive tract and are capable of fertilizing eggs for days or weeks in many species (Lake 1975). The occurrence of anatomical structures associated with prolonged sperm storage was first recognized by Van Drimmelen (1946), who described "sperm nests" in the infundibulum of the chicken (*Gallus gallus*). Further histological studies (Bobr 1962, Bobr et al. 1964, Fujii 1963, Fujii and Tamura 1963) showed infundibular storage sites to be of doubtful or secondary significance. Primary sperm storage was found to take place at the junction of the uterus (shell gland) and vagina. Since their discovery, sperm-storage sites in the uterovaginal (UV) region have been known under several names, including vaginal glands (Fujii 1963), sperm-glands (Van Krey et al. 1967), UV sperm-host glands (Gilbert et al. 1968), sperm-storage tubules (Mero and Ogasawara 1970), and UV sperm-storage glands (Burke et al. 1972). In this paper I use the last phrase, although whether or not sperm-storage sites function as true glands remains uncertain (Gilbert 1979).

Until recently, sperm-storage glands were known to occur only in three Galliformes: chicken, turkey (*Meleagris gallopavo*, Ogasawara and Fuqua 1972), and Japanese Quail (*Coturnix japonica*, F. X. Ogasawara unpubl. data). In their study of fertility in the Red-winged Blackbird (*Agelaius phoeniceus*), however, Bray et al. (1975) observed sperm in "uterovaginal glands." These authors did not illustrate or describe their finding, but a general similarity of storage-glands in Red-wings to those previously described in the chicken and turkey seems likely. The occurrence of these structures in the large majority of avian taxa remains to be determined.

In the course of a broader study of the breeding ecology of the Northern Fulmar (*Fulmarus glacialis*), I became interested in the problem of delayed fertilization and apparent sperm storage. In this paper I report the occurrence of uterovaginal sperm-storage glands in this and two other species of wild birds, the Horned Puffin (*Fratercula corniculata*) and Leach's Storm-Petrel (*Oceanodroma leucorhoa*). With this evidence of a wider taxonomic occurrence of sperm-storage glands than was previously known, I consider the ecological and behavioral significance of sperm storage in petrels and other kinds of birds, a topic that has received little attention.

MATERIALS AND METHODS

Collections were made at the Semidi Islands, Alaska (56°N, 156°W) between 17 April and 8 August 1981.

[1] Present address.

The Auk 100: 593–600. July 1983

TABLE 1. Breeding status of specimens obtained at the Semidi Islands, 1981.

Species	Collection date	Specimen number	Breeding status
Northern Fulmar	17 April	Fl	With male at well-established nest site; presumed breeder
	18 April	F2	With male at well-established nest site; presumed breeder
	5 May	F3	With male at well-established nest site; presumed breeder
	5 May	F4	With male at well-established nest site; presumed breeder
	17 May	F5	Captured while copulating
	17 May	F6	With male at established site
	4 June	F7	Egg in shell gland
	4 June	F8	Egg in shell gland
	4 June	F9	Incubating very fresh egg
	8 August	F10	Bird in wing molt; failed or prebreeder
Leach's Storm-Petrel	13 June	LSP1	Incubating fresh egg
	13 June	LSP2	Incubating fresh egg
Horned Puffin	13 June	HP1	No egg (prelaying period)
	28 June	HP2	Egg in shell gland
	28 June	HP3	No egg; status unknown

Ten fulmars, 2 Leach's Storm-Petrels, and 3 Horned Puffins were captured at their nest sites. Within 10 min of collecting a bird, I removed and preserved its oviduct in 10% buffered formalin for later histological examination. The breeding status (maturity) of fulmars collected before 31 May, when the first eggs were laid, could only be surmised from the birds' behavior and the quality of their nest sites (Table 1).

In the laboratory, 2-3-cm segments from the infundibulum, magnum, and UV region of each oviduct (Fig. 1) were embedded in paraffin and sectioned longitudinally at 6 μ. A segment of the isthmus from specimen number F6 was also prepared. One or two sections from each of two locations in each tissue sample were mounted, stained with haematoxylin and eosin, and examined microscopically.

RESULTS

Northern Fulmar.—Depending on the stage of seasonal development of the oviduct, the uterovaginal junction was located 8–25 mm from the external opening of the cloaca in Northern Fulmars. Oviducts ranged in weight from about 2 g early in the collection period to nearly 20 g around the time of laying. I had difficulty distinguishing a specialized UV region in the gross anatomy, although such a region is apparent in the laying domestic hen (Bobr et al. 1964, and pers. observation).

I failed to find any evidence of sperm storage in the infundibulum, magnum, or isthmus, but storage glands were positively identified in the UV region of all specimens collected before or shortly after oviposition. Under the microscope, the highly folded vaginal mucosa presented a dendritic pattern in cross section (Fig. 2a). Sperm-storage glands were simple, unbranched tubules extending into the lamina propria of vaginal folds in the region near the UV junction (Fig. 2b). A few glands were sectioned more or less longitudinally (e.g. Fig. 2c), but most appeared as distinct circlets or oval rings of columnar cells in cross section (Fig. 2d). Spermatozoa, if present in a tubule, were bunched at the distal end with their heads pointing away from the opening (Fig. 2c). Thus, only sections obtained near the blind end of a gland were likely to show the presence of sperm (e.g. Fig. 2e). The glands averaged 225 μ in length (SD 41.8 μ, $n = 5$) and had a mean inside diameter of 19 μ (SD 4.7 μ, $n = 20$).

Tubular glands of roughly similar proportions to sperm-storage glands were observed near the external opening of the cloaca in several specimens (Fig. 2f). Their walls were not so distinctly unicellular in thickness as those of sperm-storage glands, however, and the

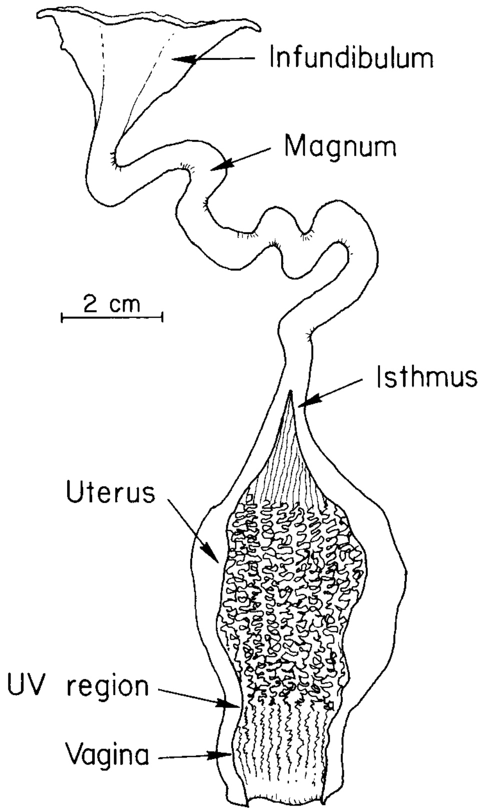

Fig. 1. Diagram of the oviduct from a Northern Fulmar as it appears around the time of oviposition, showing regions examined for the presence of sperm-storage glands.

presence of numerous clear vacuoles in these cells suggests a mucus-secreting function (F. X. Ogasawara pers. com.). The glands were more densely spaced and occupied a less convoluted vaginal mucosa than do sperm-storage glands. Sperm-storage glands also resembled the myriad shell-secreting glands in the uterine mucosa, but uterine shell glands were densely packed within large, lobular folds and frequently lacked a distinct lumen in cross section (Fig. 2g).

The presence of sperm in UV glands was confirmed in specimens F3 through F6. Sperm may have been observed in one gland from specimen F2. Specimens F1, F7, F8, and F9 all apparently lacked sperm in the UV glands, although the possibility that relatively small numbers were present cannot be excluded. I made no attempt to quantify the total amount of sperm or percentage of glands containing any, because this would have required a much larger number of sections.

Specimen F10, collected 7 weeks after the last eggs were laid, lacked UV sperm-storage glands. Vaginal and uterine folds were indistinguishable, were less branched than in the earlier specimens, and contained only glands having the general appearance of shell-secreting glands in the uteri of laying or prelaying birds (Fig. 2h).

Leach's Storm-Petrel.—UV glands matching the description of sperm-storage glands in fulmars were found in the oviducts of both Leach's Storm-Petrels (Fig. 3a, b). No spermatozoa were identified. Specimen LSP1 exhibited a major inpocketing of UV mucosa not seen in the sperm-storage area in fulmars (Fig. 3c). A simpler arrangement of folds in the UV region was present in LSP2 (Fig. 3d). Sperm-storage sites were not observed in the infundibulum or proximal magnum of Leach's Storm-Petrels.

Horned Puffin.—Sperm-storage glands were recognized in the UV region of all three Horned Puffins (Fig. 4a, b), and spermatozoa were positively identified in several glands of specimen HP3. It appeared that storage glands were less numerous in UV tissue from Horned Puffins than in that from the Northern Fulmar, although more material should be examined to confirm this. Sperm-storage glands were not found in the infundibulum or proximal magnum.

Discussion

It is now known that sperm-storage glands occur in five families of birds in four taxonomically distant orders. Although further work is needed, it appears that these structures may occur throughout Class Aves. The structure of sperm-storage glands in the three species I studied was similar to what has been described in the domestic hen. I assume the glands also have a similar physiology, a topic recently reviewed by Lake (1975) and Gilbert (1979).

The fertile period in birds may be defined as the maximum time-span over which fertile eggs are produced by an inseminated female following separation of the sexes. [This differs somewhat from Lake (1975), whose definition specified a single natural or artificial insemination as the standard for comparison. Such data are

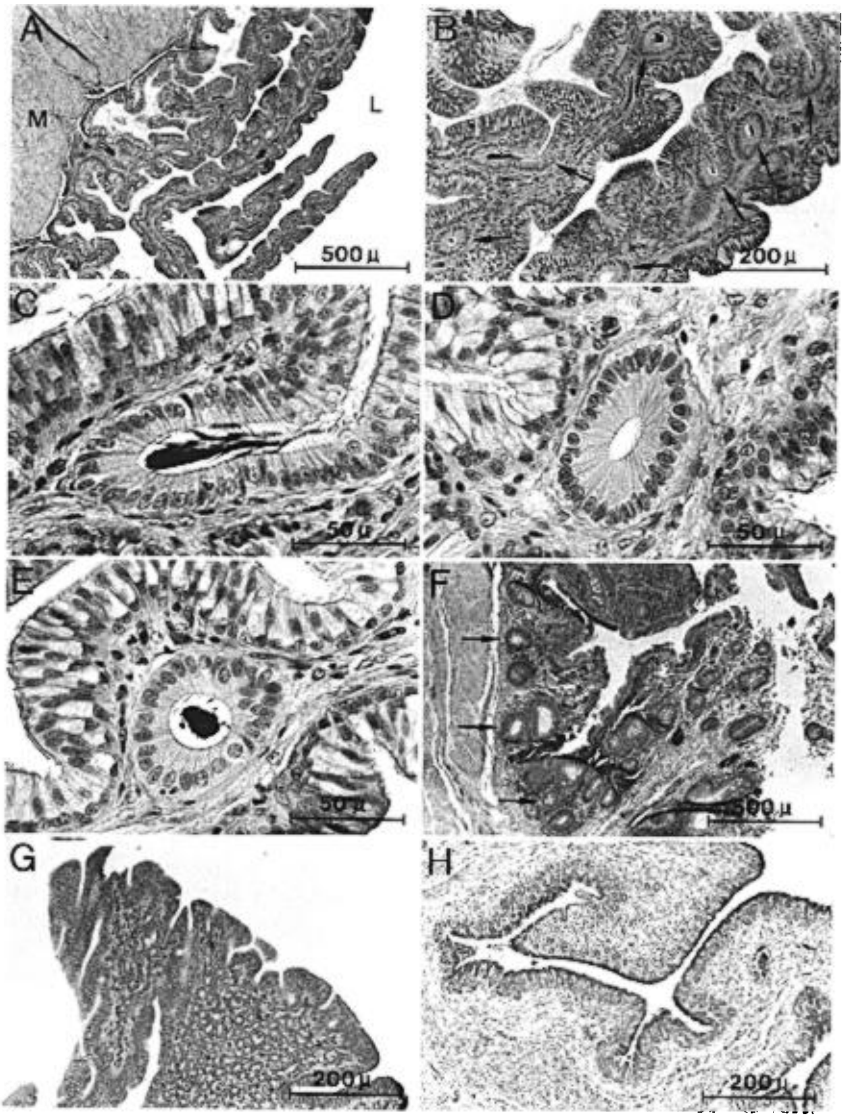

Fig. 2. Photomicrographs of the UV and adjacent regions in the oviduct of the Northern Fulmar. (A) Complex folds of the UV mucosa in specimen F6. L is lumen of oviduct; M is muscle layer of oviducal wall. (B) Magnification of UV folds with positions of sperm-storage glands indicated by arrows. (C) Magnified longitudinal section of a sperm-storage gland showing the orientation of spermatozoa; heads directed toward the blind end of the tubule. (D) Detail of an empty sperm-storage gland in cross section. Note the distinct circlet of cell nuclei by which storage glands can be recognized. (E) Cross section near the distal end of a gland containing spermatozoa. (F) Presumed mucus-secreting glands (arrows) near the external opening of the cloaca in specimen F7, to be distinguished from sperm-storage glands in the UV region. (G) Section of the uterine lining from specimen F9. Note the superficial resemblance, but greater density, of shell-secreting glands to UV sperm-storage glands. (H) Section of the vaginal or uterine region of specimen F10 in which characteristic sperm-storage glands cannot be distinguished.

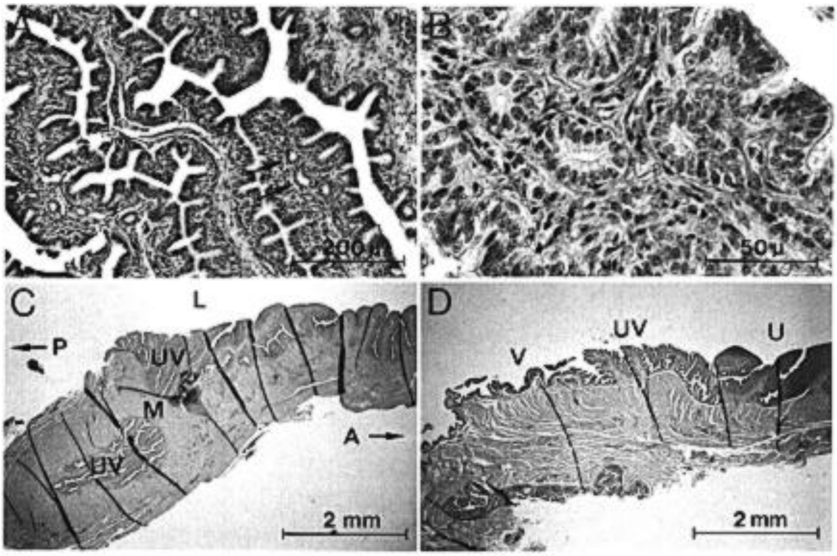

Fig. 3. Photomicrographs of UV sperm-storage area in Leach's Storm-Petrel. (A) Folded mucosa in the UV region. (B) Detail of sperm-storage glands indicated by arrows in (A). (C) Sperm-storage area of LSP1 showing an inpocketing of UV tissue. A is anterior; P is posterior; L is oviducal lumen; UV is folded UV mucosa containing sperm-storage glands; M is a bridge of muscle tissue forming the "neck" of the UV pocket. (D) Posterior end of the oviduct from LSP2 in which the sperm-storage area (UV) is clearly distinguished from vaginal folds lacking storage glands (V) and the more lobular folds of the uterus (U).

difficult to obtain for wild birds and are perhaps of doubtful ecological significance.] Despite the apparent prevalence and effectiveness of sperm storage in birds, the fertile period varies widely among species. Available data indicate a range of about 8 weeks, from 6 days in the Ring Dove (*Streptopelia risoria*, Zenone et al. 1979) to perhaps 60 days in the Grey-faced Petrel (*Pterodroma macroptera*, Imber 1976).

Regarding the ecological significance of the UV glands, Lake (1975) suggested three aspects of reproduction that may determine the selective value of sperm storage and a prolonged fertile period: clutch size, mating system, and the prevalence of renesting. In monogamous species that lay especially large clutches or lekking species in which the female may be inseminated only once during a season (e.g. Wiley 1973), the ability of the female to store spermatozoa may obviate repeated copulation as successive eggs are laid. Sperm storage might also eliminate the need for access to a male

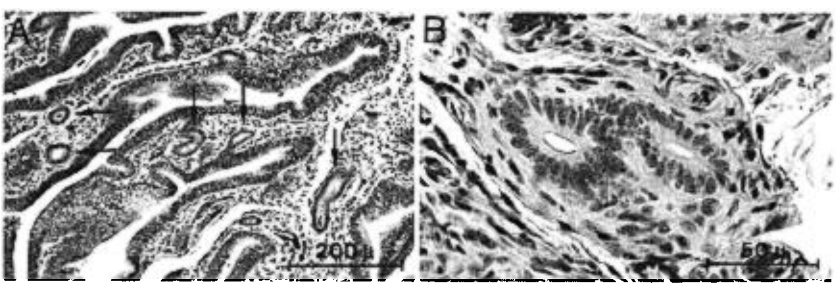

Fig. 4. Photomicrographs of UV sperm-storage glands in the Horned Puffin. (A) UV region of specimen HP3 with sperm-storage glands indicated by arrows. (B) Detail of two sperm-storage glands in cross section (specimen HP2).

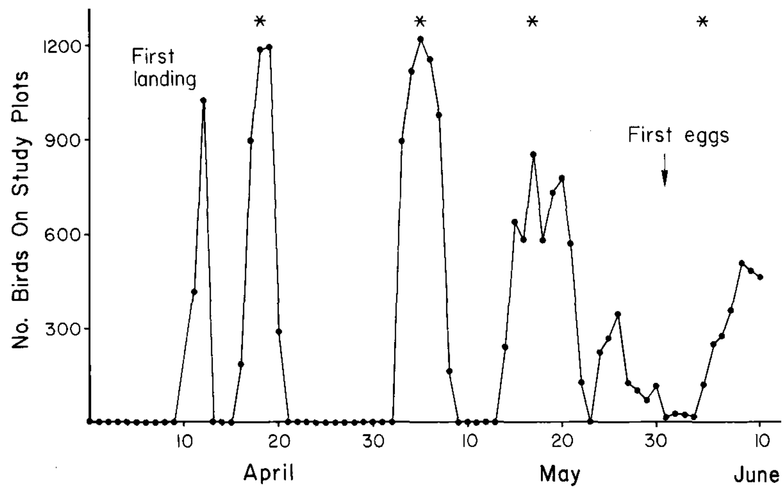

Fig. 5. Pattern of attendance at nest sites by Northern Fulmars during the prenesting period, Semidi Islands, 1981. Asterisks indicate the dates on which specimens were collected.

when renesting follows the loss of the first clutch [but see Elder and Weller (1954) and Parker (1981) for contrary evidence in the Mallard (*Anas platyrhynchos*) and Willow Ptarmigan (*Lagopus lagopus*)]. To this list I shall add the importance of sperm-storage glands in the evolution of delayed fertilization among petrels, as discussed below.

I examined the oviduct of the Horned Puffin, because there seemed to be no compelling need for sperm storage in this species. Horned Puffins are monogamous, the male and female are together before egg laying, only one egg is laid, and renesting is rare. The occurrence of sperm-storage glands in Horned Puffins suggests that evolution has occurred mainly in the physiology of the glands, not their presence or absence. Further comparative study should settle the question of whether sperm-storage glands occur universally in birds, being modified or functionally enhanced in certain groups, or are special structures independently evolved in response to one or more of the selective factors suggested above.

An adaptation to long-distance foraging observed in many petrels and their relatives (Procellariiformes) is the "pre-laying exodus" (Warham 1964). Having re-established their nest sites and pair bonds at the start of the breeding season, the females, and in some species also the males, desert the breeding area for a period of days or weeks immediately before egg laying. This behavior evidently provides a period of uninterrupted foraging during which females build the reserves required to produce a single large egg and males prepare to fast during the first long shift of incubation (Lack 1966).

Among female Northern Fulmars the prelaying exodus averages about 3 weeks (MacDonald 1977, Hatch 1979). In males, the absence is usually shorter and may be interrupted by brief visits to the nest site. A female usually lays within 24 h of returning to the colony after the exodus; her mate may or may not be present upon her arrival. To insure fertility, therefore, copulation must occur before the exodus. Most pairs engage in 20 or more successful copulations at the nest site over several days before departure, whereas copulation is rarely seen once egg laying has begun in a colony. In hundreds of hours of observation on fulmars during the prenesting period, I have never seen a copulation attempted on the water near the colonies. As the departure of male and female on the exodus is rarely synchronous (frequently days apart), it is also unlikely that the birds associate at sea. Yolk formation has only just started when a female leaves on the exodus, and it occupies most of the time she spends at sea (Hatch unpubl. data). Thus, the possibility of early ovulation with an arrested passage of the fertilized egg down the oviduct probably can be excluded. The ability to store sperm for at least 3 weeks is thus an integral feature of this species' breeding biology. Notably, there is no associated reduction in fertility. Hatchability (the percentage of eggs incubated to full term that hatch) averages about 94% (Hatch unpubl. data), which is slightly higher than the overall mean in birds (Koenig 1982).

The longest prelaying exodus known in petrels is 8–10 weeks reported for the Grey-faced Petrel (Imber 1976). Because the sequence of events during its prenesting period is similar to what I have described above, this species possibly is the extreme example of prolonged sperm storage in birds. My results indicate that Procellariiformes use mechanisms for sperm storage that are qualitatively the same as in other avian taxa. I believe UV sperm-storage glands will prove to be a common feature of the avian reproductive system. On this basis, I regard the glands as an important preadaptation that makes the prelaying exodus possible in petrels. Many petrels greatly extend the period over which spermatozoa remain viable in the oviduct, perhaps with a comparatively large investment in nutrition provided by the UV glands.

Compton and Van Krey (1979) found no difference in the number of sperm-storage glands containing spermatozoa after small and large doses of semen in the domestic fowl. They concluded that only a specific number of spermatozoa are capable of entering the glands during a given time interval (24 h in their experiment). There was some indication, however, that multiple inseminations may be required to charge the UV storage glands fully with spermatozoa in the Northern Fulmar. The first landfall of fulmars at the Semidi Islands occurred on 11 April in 1981. Over the next 6 weeks, attendance at the colony occurred in synchronized cycles (Fig. 5), which typify the pattern observed each year at the Semidis (Hatch 1979). Pairs were observed to copulate within an hour after reuniting at their nest sites on 11 April and frequently during each subsequent rendezvous before the exodus. Collections made between 17 April and 17 May (Table 1) corresponded to each of three peaks in colony attendance, and there appeared to be a buildup of sperm in UV glands over this period. Fertilization will usually have occurred by the time a female returns from the exodus, and it appeared that spermatozoa had completely evacuated the storage glands in the three specimens collected at this time.

The lack of well-defined storage glands in the bird collected on 8 August suggests these structures undergo seasonal development and degeneration. Fujii (1963) and Burke (1968), however, found no evidence of morphological changes in the UV glands related to the ovulatory cycle in the chicken.

The long period over which competing inseminations can occur exacerbates the problem of potential cuckoldry for male Northern Fulmars. Mate guarding and extra-pair copulations are observed features of the male reproductive strategy, the evolution of which is probably governed by temporal aspects of sperm storage and delayed fertilization (Hatch in prep.). There is limited, conflicting information on mechanisms of sperm precedence in domesticated birds (Warren and Kilpatrick 1929, Compton et al. 1978). Given the diversity of mating systems among wild birds and the apparent prevalence of sperm storage, such studies on a variety of species should prove most useful in understanding avian sexual behavior.

Acknowledgments

My interest in the topic of this paper developed under the academic guidance of F. A. Pitelka. The work would not have been undertaken except for the interest and freely shared expertise of F. X. Ogasawara. C. R. Grau provided early encouragement and introductions to the right people. T. Harrington taught me everything I know about the techniques of histology and gave patient assistance in the laboratory. I thank the director of the California Primate Research Center for allowing me to use laboratory facilities at the Center. My wife, M. A. Hatch, assisted in the field, and W. Bemis helped me take the photomicrographs. I thank F. A. Pitelka, F. X. Ogasawara, J. T. Burns, C. R. Grau, S. G. Pruett-Jones, and D. W. Winkler for many helpful comments on earlier drafts of the manuscript.

Literature Cited

Bobr, L. W. 1962. Oviducal distribution of spermatozoa and fertility of the domestic fowl. Unpublished Ph.D. dissertation. Davis, California, Univ. California.

———, F. W. Lorenz, & F. X. Ogasawara. 1964. Distribution of spermatozoa in the oviduct and fertility in domestic birds. J. Reprod. Fert. 8: 39–47.

Bray, O. E., J. J. Kennelly, & J. L. Guarino. 1975. Fertility of eggs produced on territories of vasectomized Red-winged Blackbirds. Wilson Bull. 87: 187–195.

Burke, W. H. 1968. Release of spermatozoa from storage sites in the hen's oviduct. Unpublished

Ph.D. dissertation. Davis, California, Univ. California.

———, F. X. OGASAWARA, & C. L. FUQUA. 1972. A study of the ultrastructure of the uterovaginal sperm-storage glands of the hen, *Gallus domesticus,* in relation to a mechanism for the release of spermatozoa. J. Reprod. Fert. 29: 29-36.

COMPTON, M. M. & H. P. VAN KREY. 1979. A histological examination of the uterovaginal sperm storage glands in the domestic hen following an insemination with variable semen dosages. Poult. Sci. 58: 478-480.

———, ———, & P. B. SIEGEL. 1978. The filling and emptying of the uterovaginal sperm-host glands in the domestic hen. Poult. Sci. 57: 1696-1700.

ELDER, W. H., & M. W. WELLER. 1954. Duration of fertility in the domestic Mallard hen after isolation from the drake. J. Wildl. Mgmt. 18: 495-501.

FUJII, S. 1963. Histological and histochemical studies on the oviduct of the domestic fowl with special reference to the region of uterovaginal juncture. Arch. Histol. Japan 23: 447-559.

———, & T. TAMURA. 1963. Location of sperms in the oviduct of the domestic fowl with special reference to storage of sperms in the vaginal gland. J. Fac. Fish. Anim. Husb., Hiroshima Univ. 5: 145-163.

GILBERT, A. B. 1979. Female genital organs. Pp. 237-360 *in* Form and function in birds (A. S. King and J. McLelland, Eds.). New York, Academic Press.

———, M. E. REYNOLDS, & F. W. LORENZ. 1968. Distribution of spermatozoa in the oviduct and fertility in domestic birds. J. Reprod. Fert. 17: 305-310.

HATCH, S. A. 1979. Breeding and population ecology of Northern Fulmars (*Fulmarus glacialis*) at Semidi Islands, Alaska. Unpublished M.S. Thesis. Fairbanks, Alaska, Univ. Alaska.

IMBER, M. J. 1976. Breeding biology of the Grey-faced Petrel *Pterodroma macroptera gouldi.* Ibis 118: 51-64.

KOENIG, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99: 526-536.

LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.

LAKE, P. E. 1975. Gamete production and the fertile period with particular reference to domesticated birds. Symp. Zool. Soc. London 35: 225-244.

MACDONALD, M. A. 1977. The pre-laying exodus of the Fulmar *Fulmarus glacialis* (L.). Ornis Scandinavica 8: 33-37.

MERO, K. N., & F. X. OGASAWARA. 1970. Dimensions of uterovaginal sperm-storage tubules of the Chicken and their possible significance in sperm release. Poult. Sci. 49: 1304-1308.

OGASAWARA, F. X., & C. L. FUQUA. 1972. The vital importance of the utero-vaginal spermhost glands for the Turkey hen. Poult. Sci. 51: 1035-1039.

PARKER, H. 1981. Duration of fertility in Willow Ptarmigan hens after separation from the cock. Ornis Scandinavica 12: 186-187.

VAN DRIMMELEN, G. C. 1946. 'Spermnests' in the oviduct of the domestic hen. J. South African Vet. Med. Assoc. 17: 42-52.

VAN KREY, H. P., F. X. OGASAWARA, & J. PANGBORN. 1967. Light and electron microscopic studies of possible sperm gland emptying mechanisms. Poult. Sci. 46: 69-78.

WARHAM, J. 1964. Breeding behaviour in Procellariiformes. Pp. 389-394 *in* Biologie antarctique symp. 1 (R. Carrick, M. Holgate, and J. Prevost, Eds.). Paris, Hermann.

WARREN, D. C., & L. KILPATRICK. 1929. Fertilization in the domestic fowl. Poult. Sci. 8: 237-256.

WILEY, R. H. 1973. Territoriality and non-random mating in Sage Grouse, *Centrocercus urophasianus.* Anim. Behav. Monogr. 6: 87-169.

ZENONE, P. G., M. E. SIMS, & C. J. ERICKSON. 1979. Male Ring Dove behavior and the defense of genetic paternity. Amer. Natur. 114: 615-626.