

FORCED COPULATION IN CAPTIVE MALLARDS III. SPERM COMPETITION

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ABSTRACT.—Previous observations of forced copulation (FC) in captive Mallards (*Anas platyrhynchos*) showed that most FC attempts were directed at females in prelaying and laying condition and that most FC's occurred in the morning when the females were leaving their nests after egg laying. In order to determine whether or not there is a physiological basis for these observed temporal patterns, sperm competition in captive Mallards was examined using artificial insemination and genetic markers. Results indicated that if a female was inseminated with two competing doses of semen at different time intervals, the proportion of progeny from the first and the second inseminations was not significantly different if these inseminations were simultaneous, 1 h, or 3 h apart. There was a preponderance of progeny (70%) from the second insemination, however, if the inseminations were 6 h apart. Insemination of females less than 1 h after egg laying resulted in 25% of the eggs laid the following morning being fertile. Only 1 of 179 eggs laid the following morning was fertile when the females were inseminated more than 1 h after egg laying.

Our experiment demonstrated that there is an insemination "window," a short period when new sperm are least likely to meet competition from sperm already in the oviduct and from sperm introduced later, and it provided a possible explanation for the observed timing of FC attempts. Received 12 May 1982, accepted 3 December 1982.

PARKER (1970: 527) defined sperm competition as "the competition within a single female between the sperm from two or more males for the fertilization of the ova." Although best known in insects (Parker 1970), this phenomenon occurs also in many other animal groups (Allison 1977, Bertram 1976, Smith in press). Among birds, sperm competition undoubtedly occurs in a number of polyandrous species, in which one female may copulate with several males (Jenni 1974), and probably occurs in a number of promiscuous species as well (Wittenberger 1979). While most species of birds are considered to be monogamous (Lack 1968) and copulations occur primarily between mates, there is evidence that sperm competition may occur in some of these species also. For example, paired females have been observed to accept or solicit copulations or to be subjected to forced copulations (FC) from males other than their mates (Gladstone 1979, McKinney et al. in press). This paper deals with one duck

species (the Mallard, *Anas platyrhynchos*) in which paired females are inseminated by males other than the mate during FC, thus providing an opportunity to investigate the mechanism of sperm competition.

Earlier papers in this series on captive Mallards documented that eggs could be fertilized by FC (Burns et al. 1980) and described temporal relations between FC and female breeding condition and behavior (Cheng et al. 1982). In the latter analysis, it was shown that almost all FC's were directed at females in the laying phase and that most FC attempts occurred in the morning hours, especially when females were detected leaving their nests. Based on the ovulation pattern and sperm-storage mechanism demonstrated in domestic chickens (Compton et al. 1978, Sturkie 1976), Cheng et al. (1982) hypothesized that Mallard males were attempting FC's at that time of the day when their sperm would compete most effectively with sperm from pair copulations.

In studying sperm-storage mechanisms of the uterovaginal (UV) glands in chickens, Compton et al. (1978) showed that, if hens were subjected to artificial insemination (AI) with semen from one type of rooster and then re-

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inseminated 4 h later with an equal amount of semen from roosters with a different genetic marker, 80% of the progeny resulted from the second insemination. If the two types of male gametes were mixed in equal proportions before AI, however, the resulting phenotypes of progeny approximated a 1:1 distribution. Data from this experiment suggest that sperm from different inseminations sequentially fill the UV glands and produce a stable stratification of sperm cells, so that the most recently inseminated sperm stay on top and mixing of sperm cells from different inseminations does not occur within a gland. Sperm from the top layer are also the first released for fertilization (DeMerritt 1979), and so most of the progeny are sired by the male that performed the most recent insemination. If a similar mechanism were to exist in the Mallard, then even though males were attempting FC on females during their laying period, sperm from infrequent FC's would be likely to be covered by sperm from repeated pair copulations and would not compete effectively in fertilizing eggs.

On the other hand, ovulation in chickens normally occurs within 15–75 min after the laying of the previous egg (Sturkie 1976). The ovulated ovum remains fertilizable for only about 15 min before albumen is deposited around the yolk (Gilbert 1971). If FC attempts were so timed that sperm from such inseminations reached the infundibulum (the site of fertilization) at the time of ovulation, they might have a good chance of fertilizing the egg that would be laid the next morning. Sperm from pair copulations later in the day would not be in time to compete for fertilization of this particular egg.

The purpose of this study was to determine whether or not (1) sperm storage and utilization mechanisms in the Mallard are similar to those in the chicken and (2) sperm introduced into the female shortly after oviposition can effectively fertilize the egg to be laid on the following morning.

GENERAL METHODS

In order to determine how sperm from different inseminations compete for fertilization of the ova, the recessive white plumage gene of the Mallard (Lancaster 1963) was used as a genetic marker. Females homozygous for this allele were artificially inseminated with semen from the homozygous dominant (wild-type plumage) males and recessive (white)

males. Thus, progeny possessing wild-type plumage could be attributed to sperm from wild-type males; those with white plumage could be attributed to sperm from recessive males.

Semen was collected from the males by the massage method of Cheng and Otis (in prep.), which is a modification of the technique developed for AI of chickens and turkeys (Burrows and Quinn 1937). Fresh undiluted semen was inseminated intravaginally by everting the oviduct (Kinney and Burger 1960). Pooled semen samples from a minimum of three males of the same genotype were used for all inseminations to reduce individual male effect. Females with a hard-shell egg in the oviduct at the time of insemination were not used. For 14 days after each series of inseminations, eggs were collected daily, identified by female and date, and stored at 10°C and 65% humidity (Cheng et al. 1980). They were then incubated in a Robbins Model IHA electric forced-air incubator and were candled on the 7th, 14th, and 23rd days to determine embryo viability. Eggs containing viable embryos were transferred on the 23rd day of incubation to individual hatching baskets located in a hatcher attached to the incubator. At the time of the first candling, any apparently infertile eggs were broken out and macroscopically classified as an early embryonic death or as infertile (Kosin 1944). Dead embryos detected during the second and third candling were also recorded. Because ducklings homozygous for the recessive white gene (i.e. those ducklings sired by white males) have yellow down, while those sired by wild-type males have the typical yellow and brown down pattern, paternity could be determined for all ducklings at hatching and for embryos that died after 19 days of incubation. The experiments were conducted at the facilities of the Department of Animal Science, University of Minnesota, St. Paul, Minnesota.

EXPERIMENT 1

A pilot study using White Pekings and Rouens (domestic breeds of Mallard) was conducted to develop AI techniques and to obtain preliminary data. We inseminated 16 White Peking (recessive) females with semen from White Peking males and Rouen (wild-type) males (and *vice versa*) at various time intervals, and the data collected (Table 1) appeared to agree with those reported for chickens (Compton et al. 1978). Problems existed with regard to the adaptiveness of White Peking females to wire-floor cages, however. Because of their body weight, some females developed foot problems, and eggs were broken as a result of females stepping on them.

To obtain more conclusive evidence on the

TABLE 1. Comparison of the phenotypic ratio of progeny following inseminations with two types of semen (Peking and Rouen) at different time intervals.

Treatment	First insemination	Second insemination	Time interval (h)	Number of progeny ^a		Ratio ^b
				White	Wild-type	
1	Peking	Rouen	1	6	5	10:12
2	Rouen	Peking	1	7	4	
3	Peking	Rouen	6	5	11	10:22 ^c
4	Rouen	Peking	6	11	5	
Controls	Mixed semen		0	23	26	(23:26)

^a Females that did not lay any fertile eggs after the inseminations were not included.

^b Ratio of the number of progeny resulting from the first insemination versus the number of progeny resulting from the second insemination.

^c $\chi^2 = 4.50$, based on the expected 1:1 ratio, $\chi^2_{0.05}$ with 1 df = 3.84.

relative effectiveness of competing inseminations at different time intervals, a further experiment on a larger scale was conducted using game-farm (GF) Mallards and domestic white (DW) Mallards. These two "breeds" were used rather than White Pekings and Rouens because of their small body size (adult DW females weighed about 1,450 g) and reliably high rate of egg production.

METHODS

Two hundred 1-day-old DW Mallard ducklings were purchased from the Pietrus Hatchery (Sleepy Eye, Minnesota) in June 1979. The Pietrus Hatchery obtained their stock from a farm in Iowa and has maintained a breeding flock of about 300 DW Mallards for four generations with a male to female ratio of 1:5. Although the DW Mallard is a different breed from the White Peking, they are homozygous for the same white plumage gene. Sixty male GF Mallard (wild-type) ducklings were also obtained from the Northern Prairie Wildlife Research Center in Jamestown, North Dakota. These GF Mallards were descendants of wild birds that were captured in 1949 at the Frost Game Farm in Wisconsin (Frost 1972, Cheng et al. 1980). The ducklings were raised together under a daily 8-h light schedule in a 12.2-m × 6.1-m floor pen until the end of January 1980, when they were moved to laying cages.

Females were housed individually in 31-cm wide × 41-cm high × 46.5-cm deep chicken laying cages. Cage-floors were slanted so that eggs laid would roll to a trough outside the cage. We kept 50 males of each breed, four to a cage, in 76-cm × 92-cm × 76-cm cages. The lighting schedule for all birds was increased to 15 h (0500–2000) of light per day, which resulted in most (75/96) of the females commencing egg production 10 days after the photoperiod was increased. Females were divided into three groups, each consisting of 24 experimental females and 6 reserves. The experimental females in each group were inseminated according to the scheme shown in Fig.

1. There were basically four treatments with four females in each treatment: (1) females were inseminated simultaneously with both GF and DW semen (8, 16, 20 and 23), (2) females were subjected to sequential AI 1 h apart (6, 7, 9, and 10), (3) females were subjected to sequential AI 3 h apart (4, 5, 11, and 12), and (4) females were subjected to sequential AI 6 h apart (2, 3, 13, and 14). Within Treatment 1, females received a single insemination consisting of 0.2 ml semen from both GF and DW males mixed in equal volume. Within each of Treatments 2, 3, and 4, two of the four females were each inseminated with 0.1 ml of pooled semen from DW males and re-inseminated with 0.1 ml of pooled semen from GF males (Part A of scheme). The other two females in each treatment were first inseminated with semen from GF males and re-inseminated with semen from DW males according to the same schedule (Part B of scheme). In cases where there was only one insemination, 0.2 ml of semen was used in order to be comparable with cases where two separate doses of 0.1 ml were given. The common dosage for AI in geese is 0.05 ml of undiluted semen (Kinney and Burger 1960, Kurbatov et al. 1976). AI dosages ranging from 0.01 to 0.025 ml of undiluted semen yield good fertility in Muscovy ducks (Huang and Chow 1974), and a dosage of 0.1 ml diluted semen (1 part of semen to 3 parts of extender) per insemination resulted in good fertility in Peking ducks (Davtyan and Starygin 1974). The dosage we were using would insure the introduction of adequate sperm numbers. It is not known how much semen is normally transferred through natural mating. In our study, the mean volume of ejaculate through the massage method was 0.12 ml (Cheng and Otis in prep.).

Treatment 1 and the reciprocal order of inseminations in the two parts of the scheme insure that any difference in the effectiveness of competition between the two types of semen can be detected and controlled. To control further for fertility differences and the remote possibility that some GF males used may have been heterozygous for the wild-type gene, 0.2 ml of each pooled semen sample was used to inseminate the eight females (1, 15, 17, 18, 19, 21,

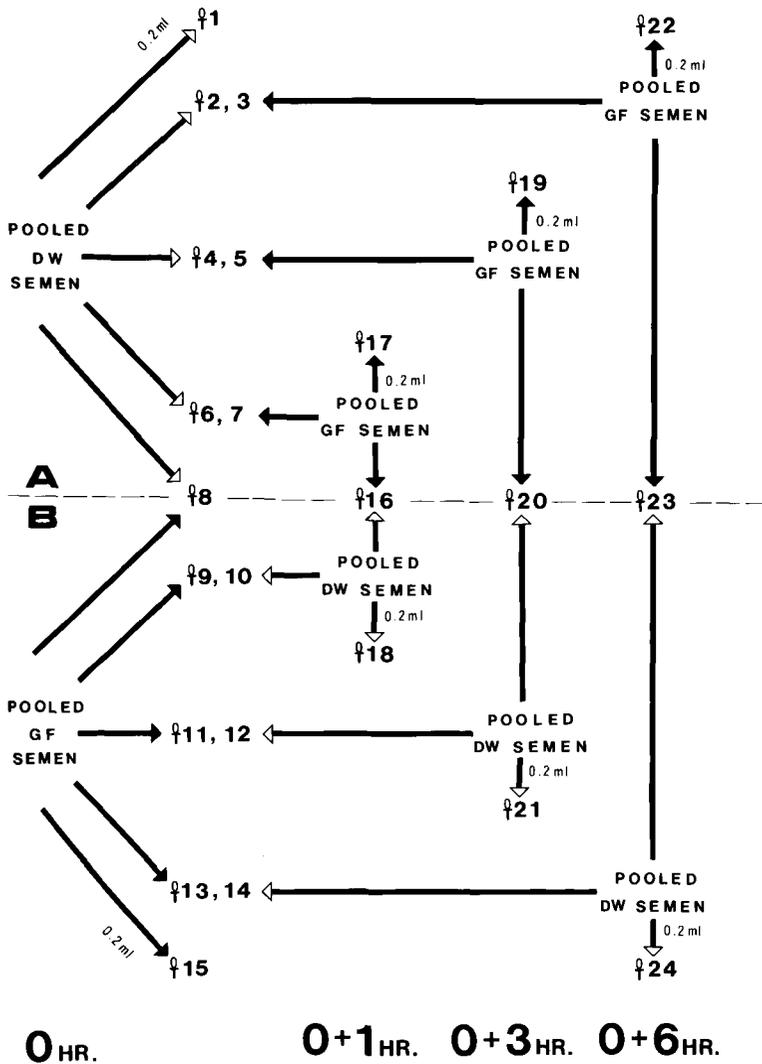


Fig. 1. Schedule of artificial inseminations. Except where specified otherwise, each female received a dose of 0.1 ml of semen per insemination.

22, and 24) not used in the four treatments. Eggs were collected for 14 days after the inseminations and then the females were randomly reassigned within groups for the next replication. The experiment was repeated once with all 3 groups of females and again with only 2 groups (i.e. altogether 8 replications). In total, 2,338 eggs were set for incubation.

RESULTS

Fertility and hatchability.—Data collected from control females 1, 15, 17, 18, 19, 21, 22, and 24 of each replication showed that the hatchability of 206 eggs fertilized by DW semen (86%)

was not significantly different from the hatchability of those (148) fertilized by GF semen (85%). The fertility of eggs from females over the 14-day period after insemination with GF semen, however, was only 47.4% (148/312) and was significantly lower than that of eggs from those females inseminated with DW semen (61.5%; 206/335) (Cheng and Otis in prep.). Apparently, this was mainly caused by differences in duration of fertility over the 14-day period. Only one of the eggs collected on the first day after AI was fertile. Fertility of eggs from females inseminated with DW semen was

TABLE 2. Comparison of phenotypic ratio of progeny for days 2–7 following sequential AI with genetically marked (GF, DW) semen.

Treatment	Sequence of AI	Time interval (h)	Number of progeny		White vs. wild-type ratio	First AI vs. second AI ratio
			White	Wild-type		
1	Mixed	0	52	49	52:49	(52:49)
2	GF-DW	1	12	12	33:36	33:36
	DW-GF	1	21	24		
3	GF-DW	3	16	21	40:37	45:32
	DW-GF	3	24	16		
4	GF-DW	6	20	5	38:41	23:56 ^a
	DW-GF	6	18	36		

^a $\chi^2 = 13.78$, based on the expected 1:1 distribution, $\chi^2_{0.01}$ with 1 df = 6.63.

above 80% from day 2 to day 8, while that from females inseminated with GF semen was only above 80% from day 2 to day 5. Thereafter, fertility of eggs from these females declined steadily.

Phenotypic ratio of progeny.—As there were no significant differences within each treatment in the phenotypic ratio of progeny between replications, data from all eight replications were pooled for analysis. Because of the difference in the duration of fertility between the two types of males, data for days 2 to 7 and days 8 to 14 are summarized separately and presented in Tables 2 and 3, respectively. Equal weight was given to each individual female in calculating the progeny phenotypic ratio. The phenotypic ratio of wild-type GF progeny to white progeny in all four treatments did not differ from the expected 1:1 ratio for the period of days 2–7 (Table 2). On the other hand, there were significantly more ($\chi^2 = 20.3$, df = 1, $P <$

0.005) white progeny than wild-type progeny in the second period (days 8–14, Table 3). This is consistent with the observations from control females that the duration of fertility was longer for DW than for GF semen.

To avoid the bias caused by the difference in the duration of fertility between the two types of semen, only data collected during the period from 2 to 7 days postinsemination were considered in estimating the proportion of progeny resulting from sequential AI. As shown in Table 2, the phenotypic ratio of progeny resulting from AI with mixed semen (Treatment 1) and inseminations 1 h apart (Treatment 2) approximated the expected 1:1 ratio and was consistent with the observations made in the pilot study. Furthermore, the 1:1 ratio was maintained even when the inseminations were 3 h apart (Treatment 3). Following sequential inseminations 6 h apart (Treatment 4), however, significantly more progeny (70.9%) were

TABLE 3. Comparison of phenotypic ratio of progeny for days 8–14 following sequential AI with genetically marked (GF, DW) semen.

Treatment	Sequence of AI	Time interval (h)	Number of progeny		White vs. wild-type ratio ^a	First AI vs. second AI ratio
			White	Wild-type		
1	Mixed	0	18	16	18:16	(18:16)
2	GF-DW	1	6	8	13:23	15:21
	DW-GF	1	7	15		
3	GF-DW	3	12	8	36:15 (8.65)**	32:19
	DW-GF	3	24	7		
4	GF-DW	6	33	7	66:15 (32.11)**	40:41
	DW-GF	6	33	8		
Total					133:69 (20.28)**	

^a χ^2 (in parentheses) based on the expected 1:1 distribution; ** $P < 0.01$.

TABLE 4. Fertility of eggs from inseminations timed with egg laying.

Time of insemination	Groups	Number of eggs laid next morning	Number of eggs fertile
More than 1 hour after laying	Expt. 1	168	1
	Expt. 2		
	Control	7	0
	Re-insemination	4	0 ^a
	Total	179	1
Less than 1 hour after laying	Expt. 2		
	Treatment 1	13	3
	Re-insemination	7	5 ^a
	Treatment 2	12	1
	Re-insemination	4	0 ^a
Total	36	9	

^a Number of eggs fertilized by sperm from last insemination.

attributed to the second of the two inseminations.

EXPERIMENT 2

Most females laid eggs between 0500 and 0900 each day. In Experiment 1, the first insemination was carried out at 1000, which would be an hour or more after egg laying for most females. Of the 168 eggs collected on the morning following the day of inseminations, only one egg was fertile. The purpose of Experiment 2 was to determine whether or not eggs laid the morning following the day of inseminations could be fertilized if females were inseminated *within* an hour after laying.

METHODS

Fifty DW females that had been laying infertile eggs (i.e. females that had not been subjected to AI within a 2-week period) were used. These birds were under the same 15-h light schedule as those in Experiment 1. Laying time for each female was recorded in the morning, and 20 females were individually inseminated within 1 h after laying with 0.2 ml of pooled semen from DW males (Treatment 1). Another 20 females were inseminated with 0.2 ml of pooled semen from GF males, also within 1 h after laying (Treatment 2). The remaining 10 females were used as controls and were inseminated during the period between 1–2 h after their laying.

Three days after the first set of inseminations, laying times for these females were again recorded. Females that had been inseminated with DW semen 3 days previously (Treatment 1) were re-inseminated with GF semen and females in Treatment 2 were re-inseminated with DW semen within 1 h after laying.

RESULTS

The results of Experiment 2 are summarized in Table 4. Fourteen of the 20 females inseminated with DW semen in Treatment 1 laid in the morning following the day of AI, and 3 of the 14 eggs were fertile. Subsequent data showed that one of the females did not lay any fertile eggs during the 1-week period after the inseminations, and her record was excluded from the summary of data. Therefore, in effect, 3 of 13 eggs (23.1%) were fertile.

Of the 20 females assigned for Treatment 2, we were able to observe laying time for only 18 on the morning of AI. Therefore only 18 females were inseminated with semen from GF males. Of the 13 eggs collected the morning after, only 1 was fertile. One female in this group was infertile, and her record was excluded (i.e. in effect, 1 of the 12 eggs (8.3%) was fertile).

Seven control females were inseminated more than an hour after their laying, and none of the eggs laid the following morning was fertile.

For re-inseminations 3 days later, we were able to record laying time for 14 of the 20 females from Treatment 1 (females inseminated with DW semen). Eight eggs were collected from the 14 females inseminated with GF semen. One egg was from the infertile female, and we hatched out 5 wild-type ducklings and 2 white ducklings. Sperm from this later insemination fertilized 5 of the 7 eggs laid the morning after AI despite the presence of sperm from previous inseminations in the UV glands.

Time of laying was recorded for 12 females

from Treatment 2. These females were re-inseminated with DW semen and five eggs were collected the following morning. One embryo died within the first week of incubation, thereby precluding determination of its phenotype. Of the remaining four eggs, all produced wild-type ducklings. None of the four eggs was fertilized by sperm from the last insemination. In total, with semen from previous inseminations already present in the oviduct, sperm from the last insemination fertilized 5 of the 11 eggs (45.5%) laid the following morning.

Five of the control females were re-inseminated between 1 and 2 h after laying. Of the four eggs collected and hatched, none was fertilized by the last insemination.

Combining the data from both treatments and all inseminations, it was found that sperm inseminated within an hour after laying fertilized 9 of 36 eggs (25%) laid the morning after the day of AI (Table 4).

DISCUSSION

Some birds with large clutch sizes (e.g. chickens and turkeys) have sperm-storage glands in the oviduct, in which the functional capacity of the sperm is prolonged and from which sperm are released (Lorenz 1966, Compton and Van Krey 1979). Poultry breeders have known for a long time that sperm competition can take place in chickens and turkeys, and a good deal of experimentation on this topic has been carried out in conjunction with maximizing fertility by AI (e.g. Allen and Champion 1955, Payne and Kahr 1961, Reinhart and Jerome 1971, Lake 1975, Classen and Smith 1975, Compton et al. 1978, DeMerritt 1979). Many studies indicated that, in general, the most recent of competing inseminations is likely to be the most effective in fertilizing eggs, not only because fertility declines with the age of sperm in the UV glands but also because of the way these glands are filled and how sperm are subsequently released. Domestic Mallard females can store viable sperm for up to 17 days (Elder and Weller 1954, Ash 1962), and data from four domestic and semi-domesticated breeds of Mallard in our study showed that sperm competition also takes place in this species in a way similar to that in chickens and turkeys. Sperm from the more recent of two competing inseminations as close as 6 h apart fertilized 70% of the eggs laid subsequently. Sperm from inseminations 1 h and 3 h apart probably mixed in the oviduct before entering the UV glands and resulted in an equal probability of fertilizing ova in subsequent ovulations.

Observations of captive Mallards showed that the frequency of apparently successful FC was low compared to the frequency of pair copulations (Cheng et al. 1982). Therefore, a dose of semen from FC probably has to compete with more than one dose of semen from pair copulations during the prelaying and laying period of the female. Near the time of ovulation, however, recently inseminated sperm can traverse the UV junction and reach the infundibulum within a few minutes (Mimura 1939, Bobr et al. 1964, Howarth 1971). This is the only time when sperm transport in the oviduct is not obstructed by the presence of an egg (Morzenti et al. 1978). Data from Experiment 2 showed that sperm from 9 of 36 (25%) inseminations administered within an hour after laying were successful in fertilizing the egg to be laid the next morning. Although the percentage of success was not high, this result showed that there is an insemination "window," a short period when new sperm are least likely to meet competition from sperm already in the oviduct and from sperm introduced later.

There is some evidence to suggest that male Mallards are timing their FC attempts in relation to this especially favorable period. In a flight-pen study, most FC attempts occurred during the morning hours (when eggs are laid), and they were directed especially at females leaving their nests (Cheng et al. 1982). The time intervals between laying, ovulation, and departure from the nest have not been studied in ducks, but there is some information on the total time spent at the nest on the days when eggs are laid. Northern Shovelers (*Anas clypeata*) studied by Afton (1977, 1980) spent 94–107 min on the nest during laying of the first three eggs of the clutch, but thereafter they spent increasingly longer periods on the eggs (3–4 h for the 4th and 5th eggs, up to about 12 h on the day the last eggs were laid). On three occasions, Afton (1977) flushed a female 1–2 h after her arrival at the nest and found that a new egg had already been laid, suggesting that laying occurs soon after the bird arrives. Data for Mallards for the last half of the laying period (Caldwell and Cornwell 1975) suggest a similar pattern of increasing duration of nest

attendance during laying. These findings suggest that, when males are successful in forcing copulation on females leaving the nest, these inseminations might coincide with the favorable postovulation "window" only on the first few days of laying. This possibility deserves further study.

If FC is an evolved strategy and is effective in fertilizing eggs, mate-guarding to forestall FC attempts would be expected as a counter-adaptation. We do know that males attempt to defend their mates by fighting or trying to dislodge males attempting FC (McKinney et al. in press), but, when many males are involved in FC attempts on the same female simultaneously, this is not always effective in preventing FC. Whether the mate has additional strategies to reduce the probability of eggs being fertilized by sperm deposited by FC is largely an unexplored question. Such strategies could revolve around the frequency and timing of pair copulations (PC). There is no good information, however, on the timing and frequency of PC in relation to female reproductive physiology in Mallards. Paired males frequently solicit copulation from their mates, but few are successful. Observations of Mallards (Barrett 1973, Barash 1977) and several other dabbling ducks (McKinney et al. in press) indicate that paired males sometimes force copulation on their own mates after they have been subjected to FC assaults. Our findings on sperm competition suggest that a prompt "forced pair copulation" (FPC) would be especially advantageous for the paired male if FC had occurred during the postovulation period when fertilization takes place. At other times, however, the mate might benefit more by waiting and performing PC after an interval of several hours. Apparently FPC's are not invariably performed after FC's, and, if the female resists, the attempt to mount is often aborted.

Our experiments demonstrated that sperm competition can take place in Mallards and provided a physiological basis for a possible explanation of some of the temporal patterns of FC behavior observed in our flight pens. These experiments raise interesting questions about the degree to which behavioral strategies of males are "finely tuned" to the reproductive physiology of females, and, in particular, they lead to predictions that can guide future behavioral studies of PC, FC, and FPC.

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LITERATURE CITED

- AFTON, A. D. 1977. Aspects of reproductive behavior in the Northern Shoveler. Unpublished M.S. thesis. Minneapolis, Minnesota, Univ. Minnesota.
- . 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* 82: 132-137.
- ALLEN, C. J., & L. R. CHAMPION. 1955. Competitive efficiency of turkey sperm. *Poultry Sci.* 34: 1598-1604.
- ALLISON, A. J. 1977. Flock mating in sheep. II. Effect of number of ewes per ram on mating behavior and fertility of two-tooth and mixed-age Romney ewes run together. *New Zealand J. Agr. Res.* 20: 123-128.
- ASH, W. J. 1962. Studies of reproduction in ducks. 1. The duration of fertility and hatchability of White Pekin duck eggs. *Poultry Sci.* 41: 1123-1126.
- BARASH, D. P. 1977. Sociobiology of rape in Mallards (*Anas platyrhynchos*): responses of mated male. *Science* 197: 788-789.
- BARRETT, J. 1973. Breeding behavior of captive Mallards. Unpublished M.S. thesis. Minneapolis, Minnesota, Univ. Minnesota.
- BERTRAM, B. C. R. 1976. Kin selection in lions and in evolution. Pp. 281-301 in *Growing points in ethology* (P. P. G. Bateson and R. A. Hinde, Eds.). Cambridge, England, Cambridge Univ. Press.
- BOBR, L. W., F. X. OGASAWARA, & F. W. LORENZ. 1964. Distribution of spermatozoa in the oviduct and fertility in domestic birds. II. Transport of spermatozoa in the fowl oviduct. *J. Reprod. Fert.* 8: 49-58.
- BURNS, J. T., K. M. CHENG, & F. MCKINNEY. 1980. Forced copulation in captive Mallards. I. Fertilization of eggs. *Auk* 97: 875-879.
- BURROWS, W. H., & J. P. QUINN. 1937. The collection of spermatozoa from the domestic fowl and turkey. *Poultry Sci.* 16: 19-24.
- CALDWELL, P. J., & G. W. CORNWELL. 1975. In-

- cubation behavior and temperatures of the Mallard Duck. *Auk* 92: 706-731.
- CHENG, K. M., R. N. SHOFFNER, R. E. PHILLIPS, & F. B. LEE. 1980. Reproductive performance in wild and game-farm Mallards. *Poultry Sci.* 59: 1970-1976.
- , J. T. BURNS, & F. MCKINNEY. 1982. Forced copulation in captive Mallards. II. Temporal factors. *Anim. Behav.* 30: 695-699.
- CLASSEN, H. L., & J. R. SMITH, JR. 1975. Competitive fertilization in the domestic fowl. *Poultry Sci.* 54: 1748.
- COMPTON, M. M., & H. P. VAN KREY. 1979. Emptying of the uterovaginal sperm storage glands in the absence of ovulation and oviposition in the domestic hen. *Poultry Sci.* 58: 187-190.
- , ———, & P. B. SIEGEL. 1978. The filling and emptying of the uterovaginal sperm-host glands in the domestic hen. *Poultry Sci.* 57: 1696-1700.
- DAVYAN, A. D., & M. I. STARYGIN. 1974. Artificial insemination in duck production. Proc. and Abs. 15th World's Poultry Congr. New Orleans: 384-385.
- DEMERRITT, R. J. 1979. The role of the uterovaginal junction in sperm cell storage and release in the domestic fowl. *Poultry Sci.* 58: 1049.
- ELDER, W. H., & M. W. WELLER. 1954. Duration of fertility in the domestic Mallard hen after isolation from the drake. *J. Wildl. Mgmt.* 18: 495-502.
- FROST, J. 1972. Observations from commercial waterfowl producers. Pp. 71-72 in Symposium for the role of hand-reared ducks in waterfowl management. Dundee, Illinois, Max McGraw Wildl. Found.
- GILBERT, A. B. 1971. Transport of eggs through the oviduct and oviposition. Pp. 1345-1352 in Physiology and biochemistry of the domestic fowl (D. J. Bell and B. M. Freeman, Eds.). New York, Academic Press.
- GLADSTONE, D. E. 1979. Promiscuity in monogamous colonial birds. *Amer. Natur.* 114: 545-557.
- HOWARTH, B., JR. 1971. Transport of spermatozoa in the reproductive tract of turkey hens. *Poultry Sci.* 50: 84.
- HUANG, H. H., & T. C. CHOW. 1974. Artificial insemination in mule duck production. Proc. and Abs. 15th World's Poultry Congr. New Orleans: 261-262.
- JENNI, D. A. 1974. Evolution of polyandry in birds. *Amer. Zool.* 14: 129-144.
- KINNEY, T., & R. E. BURGER. 1960. A technique for the insemination of geese. *Poultry Sci.* 39: 230-232.
- KOSIN, I. L. 1944. Macro- and microscopic methods of detecting fertility in unincubated eggs. *Poultry Sci.* 23: 266-269.
- KURBATOV, A. D., P. G. TSARENKO, & I. I. POPOV. 1976. Improving artificial insemination in geese. Proc. 8th Intern. Congr. Anim. Reproduction and Artificial Insemination, Cracow 6: 1009-1012.
- LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen & Co.
- LAKE, P. E. 1975. Gamete production and the fertile period with particular reference to domestic birds. Symp. Zool. Soc., London 53: 225-244.
- LANCASTER, F. M. 1963. The inheritance of plumage color in the common duck. *Bibliographica Genetica* 29: 317-404.
- LORENZ, F. W. 1966. Behavior of spermatozoa in the oviduct in relation to fertility. Pp. 39-43 in Physiology of the domestic fowl (C. Horton-Smith and E. C. Amorosa, Eds.). Edinburgh, Oliver & Boyd.
- MCKINNEY, F., S. R. DERRICKSON, & P. MINEAU. In press. Force copulation in waterfowl. Behaviour.
- MIMURA, H. 1939. On the mechanism of travel of spermatozoa through the oviduct in the domestic fowl, with special reference to artificial insemination. Sonderabdruck and Okjimas Folia Anatomica Japonica. 17(5). [Cited by Sturkie 1976.]
- MORZENTI, A., F. X. OGASAWARA, & C. L. FUGUA. 1978. The relationship of infundibula fluid to the avian sperm transport mechanism. *Poultry Sci.* 57: 1173.
- PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in insects. *Biol. Rev.* 45: 525-567.
- PAYNE, L. F., & A. J. KAHR. 1961. Competitive efficiency of turkey sperm. *Poultry Sci.* 40: 1598-1604.
- REINHART, B. C., & F. N. JEROME. 1971. Competition between the pooled spermatozoa of two breeds of sires in fertilization. *Poultry Sci.* 50: 1623.
- SMITH, R. L. (Ed.). In press. Sperm competition and the evolution of animal mating systems. New York, Academic Press.
- STURKIE, P. D. 1976. Avian physiology, 3rd ed. New York, Springer-Verlag.
- WITTENBERGER, J. F. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in Handbook of behavioral neurobiology, Vol. 3. Social behavior and communication (P. Marler and J. Vandenbergh, Eds.). New York, Plenum.