ROLE OF THE PROCTODEAL GLAND FOAM OF MALE JAPANESE QUAIL IN NATURAL COPULATIONS

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ABSTRACT.—Male Japanese Quail (*Coturnix japonica*) produce a thick foam from the proctodeal gland of the cloaca that is mixed with semen and inseminated into the female during copulation. We examined the effect of foam on fertility in natural copulations. In 2-male/5-female mating groups, fertility of intact males was 98% and fertility of males whose proctodeal glands were cauterized (non-foam-producing) was 26%. When an intact male competed with a non-foam-producing male, the intact males sired 99% of the progeny. We demonstrated that the presence of foam, whether artificially placed or naturally placed, extended the duration of fertility of those females fertilized. In copulations without foam, or with artificially placed foam, the proportion of females fertilized decreased significantly compared with copulations by intact males where foam was naturally placed in the proctodeum of the females (and not in the distal part of the oviduct as chicken males do when they inseminate hens).

We believe that foam acts as a medium for sperm transport along the oviduct. Why foam exists in its present form and not as part of seminal fluid, and why the foam-semen mixture is deposited in the proctodeum and not in the distal oviduct, are questions that remain.
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ADULT male Japanese Quail (*Coturnix japonica*, American Ornithologists' Union 1983) and Common Quail (*C. coturnix*) produce a thick foam from the proctodeal gland (King 1981, Klemm et al. 1973) of the cloaca (Coil and Wetherbee 1959, Ikeda and Taji 1954, Nagra et al. 1959). The secretion of the gland is a viscous glycomucoprotein that apparently foams when it interacts with CO_2 and H_2 produced by cloacal bacteria (*Escherichia coli* and *Proteus mirabilis*) that metabolize glucose in the secreted mucoid (McFarland et al. 1968). Although foam production is at present known only in *Coturnix*, a similar glandular tissue has been found in chickens and turkeys (King 1975, 1981; Komarek 1970) and is thought to produce a "frothy fluid" (Fujihara and Nishiyama 1984, Fujihara et al. 1985). The frothy fluid is a lymph-like fluid secreted from surface tissue near the papilla with a negligible amount of foam from the proctodeal gland (Fujihara et al. 1987). There is still controversy as to whether the origin and the function of the glandular tissue in the turkey and chicken are similar (Fujihara et al. 1987, Bakst and Cecil 1986, Lake pers. comm.). Similar tissue has been found in the same area of the cloaca in ducks and geese (Komarek 1971), and Hatch (1983) also found glandular tissue in Northern Fulmar (*Fulmarus glacialis*) which he thought similar to that of the proctodeal gland. The tissue in these species have not developed into functional and foam-producing glands.

The development of the gland and the production of foam in *Coturnix* is dependent on testosterone stimulation (Sachs 1967, Balthazart et al. 1979, Massa et al. 1980). There are several hypotheses regarding the function of the foam. Perez and Juarez (1966) thought it prevented postcopulatory sperm leakage from the female. Renzoni (1968) suggested that foam was a lubricant for the male's phallus. Schleidt and Shalter (1972) argued that foam was used by the male as a territorial marker. No conclusive evidence supports any of these hypotheses (King 1981). Foam is most commonly thought to be an aid to reproduction (Ikeda and Taji 1954, Klemm et al. 1973, McFarland et al. 1968, Ogawa et al. 1974, Wetherbee 1961) because it is passed on to the female along with semen during copulation and its production is testosterone-dependent (Sachs 1969, Adkins 1974). However, Marks and Lepore (1965) and Lepore and Marks (1966) obtained good fertility by artificial insemination without mixing foam with the inseminated semen.

In order to determine the function of foam in reproduction in the Japanese Quail, we studied the effect of foam on fertility under natural

copulations. Subsequently, we generated and tested hypotheses concerning the role foam may play (Cheng et al. 1989).

MATERIALS AND METHODS

Wildtype (UBC-A) and white plumage (UBC-W) Japanese Quail were obtained from the Quail Genetic Stock Centre at the University of British Columbia. White plumage is recessive to wildtype (Roberts et al. 1978) and is used as a genetic marker to determine paternity of progeny from the mating groups. The wildtype and white phenotypes can be distinguished after 10 days of incubation and paternity determined.

EXPERIMENT 1

Birds were raised in mixed sex and genotype groups from hatching until 4 weeks of age. Males were then separated from the females and only white females were maintained for the experiment. At 4 weeks of age, before the proctodeal glands became fully developed and functional, the proctodeal glands of 30 males from each line (UBC-A and UBC-W) were destroyed permanently by electric cautery (Hickman 1984). After application of local anesthetic (Xylocaine), a 1-cm cut was made longitudinally along the midline of the dorsal wall of the cloaca starting from the dorsal lip. Insulated forceps were used to keep the surface exposed, and cautery was done with a hyfrecator operating at 90 volts. Fifteen males from each line were sham-operated. Cauterization was performed rather than surgical removal to minimize distortion of the cloacal area when removing the glands. To test each cauterized male for fertility before the start of the experiment, it was housed with a female (not an experimental bird) for 6 days. Three males from pairs where all the eggs were infertile were not used for the experiment.

At 8 weeks of age, we distributed the experimental birds into 3 replications, each consisting of 4 treatment groups: (1) one cauterized UBC-A male, and one sham-operated UBC-W male, with 5 UBC-W females; (2) one cauterized UBC-W male, and one sham-operated UBC-A male, with 5 UBC-W females; (3) one UBC-A male and one UBC-W male, both cauterized, with 5 UBC-W females; and (4) one UBC-A male and one UBC-W male, both sham-operated, with 5 UBC-W females. Each group was housed in a 122 cm × 92 cm × 46 cm high floor pen with wood shavings litter.

The experiment lasted 8 weeks. To minimize bias due to any particular male, 2 sets of males were used in rotation every 2 weeks so that the first set of males was used during weeks 1, 2, 5, and 6; and the second set was used during weeks 3, 4, 7, and 8. Eggs were collected daily, identified, and incubated artificially in a Jamesway incubator. Phenotypes of the progeny were recorded and the percentage of progeny sired by foam-producing and non-foam-producing males was determined. Fertility, hatchability, and percentage of embryonic death were calculated.

We followed 2 of the 3 replications to determine differences in mating behavior between cauterized and sham-operated males, and between UBC-A and UBC-W males. Eighteen 20-min observations were made on each of the 8 pens. Observations were carried out by the same observer and were divided between the morning, afternoon, and evening periods over the 8 weeks of the experiment. We recorded mating behavior, especially frequency of completed copulations (male bending his tail around the tail of the female with apparent cloacal contact and an obvious thrust of the lower body of the male before dismounting).

Fertility and hatchability data were analyzed by analyses of variance. Mating frequencies were analyzed by ANOVA with repeated measures (Snedecor and Cochran 1980). Because in all treatment groups a UBC-A male was competing with a UBC-W male for the 5 females, their mating behaviors were not independent. Higher frequency of mating activities by one male usually resulted in lower mating frequency of the competing male in the same period. Statistical comparisons of mating frequency between foam-producing and non-foam-producing males were therefore restricted to within-genotype comparisons. Factors entered into the analyses were replications, condition of the male (foam-producing or non-foam-producing), condition of the competing male (foam-producing or non-foam-producing), and all the two-way interactions. Time of day and 3-way interactions involving the time of day were factors in the subplot. All percentages were arcsine transformed before the analyses.

EXPERIMENT 2

Six "fertility-tested," cauterized males and 6 foam-producing (sham-operated) males from each of UBC-A and UBC-W lines were used in staged copulations. In addition, 10 males of each line were maintained for their foam. Thirty-two UBC-W females that were laying infertile eggs were housed in individual 30 cm × 50 cm × 25 cm high wire cages. All the males were caged individually to prevent fighting and homosexual copulations (Adkins 1974).

The experiment consisted of 40 replications of the 4 treatments: (1) female was allowed to copulate with a non-foam-producing male; (2) female was allowed to copulate with a foam-producing male; (3) female was allowed to copulate with a non-foam-producing male and foam was artificially placed in the female's oviduct after copulation; and (4) foam was artificially placed in the female's oviduct and female was then allowed to copulate with a non-foam-producing male.

The experiment was conducted in the evening after the experimental females had laid their eggs. Within 25 min after egg laying, a male of the appropriate

TABLE 1. Fertility, hatchability of fertile eggs, and number of progeny sired by different types of males in the experimental pens. For comparison within column, means followed by different letters are significantly different.

Treatment	Type of UBC-W male	Type of UBC-A male	Eggs set (*n*)	Fertility** (%)	Hatch* (%)	Chicks typed (*n*)	White progeny** (%)
1	foam	foamless	633	76B	74B	418	99D
2	foamless	foam	660	73B	76B	424	1A
3	foamless	foamless	696	26A	53A	109	26B
4	foam	foam	666	98C	70B	540	52C

* $P < 0.05$, ** = $P < 0.01$.

type was placed in the female's cage and remained until a completed copulation occurred. If the male did not make an attempt to mount the female after 15 min, a different male of the same type was used. If two successive males failed to copulate with the female, or if only questionable contacts were made, the female was not used for that replication. After copulation, the male was removed to its own cage. A small sample of the cloacal fluid from the female was obtained with a small vinyl spatula and examined microscopically for sperm. Eggs from the female were collected for the following 10-day period, identified by female and date, and artificially incubated to determine fertility.

Because there were only 32 females available and not all the females were in egg production, females were recycled on the 11th day after the previous copulation. In order to detect any carryover fertility by the previous male, a male of the different line from the previous male was always used. In cases where foam was artificially placed in the female, foam was always obtained from a male of a different line from the male that performed the copulation. Any fertilization as a result of the unlikely contamination of the foam with sperm would then be detected.

The experiment lasted 16 weeks and a total of 40, 35, 40, and 40 copulations were staged for treatments 1, 2, 3, and 4, respectively.

RESULTS

Fertility, hatchability, and progeny phenotypes.—There was no significant difference among the 3 replications in the traits measured in Experiment 1. Fertility was highest in pens where both males produced foam, and lowest in pens where both males did not (Table 1). Hatchability of fertile eggs was significantly lower in pens with two non-foam-producing males. In pens where one male produced foam and one male did not, 99% of the progeny were sired by the foam-producing male. In pens where both males were foam-producing, UBC-W males sired as many progeny as UBC-A males (52% and 48%, respectively), but in pens where both males did not produce foam, UBC-W males sired only 26% of the progeny.

Mating frequencies.—UBC-A males without foam exhibited significantly higher frequencies of mounting attempts and completed copulations compared with UBC-A males that produced foam (Table 2). A significant ($P < 0.05$) time by condition of male interaction indicated that although the frequency of mating attempts by foam producing UBC-A males were significantly lower during the afternoon period, non-foam-producing UBC-A males exhibited high frequencies during all three periods of the day. Other interaction terms were not significant. Whether the competing male produced foam or not had no significant effect on the mating frequency of UBC-A males. The mating frequencies were not significantly different between normal and cauterized UBC-W males. Although the differences were not compared statistically, non-foam-producing UBC-A males attempted and completed about three times as many copulations as non-foam-producing UBC-W males (0.36 vs. 0.12).

TABLE 2. Frequency of mating attempts (MA) and completed copulations (CC) per male per observation period (20 min).

Types	UBC-A male		UBC-W male	
	MA	CC	MA	CC
Foam-producing	0.29*	0.16*	0.18	0.15
Foamless	0.53	0.36	0.19	0.12

* $P < 0.05$, within column comparisons.

Frequency of sperm transfer during copulation.—The frequencies of sperm transfer during copulation by normal and cauterized males were not different (Table 3). We observed sperm in 27 of 64 (42%) cloacal samples obtained from

TABLE 3. Occurrence of sperm transfer during copulations by experimental and normal males.

Treatments	Sperm	No sperm
Non-foam-producing males		
1. Copulation, no foam	11	12
3. Copulation, then foam	8	11
4. Foam, then copulation	8	14
Sham-operated males		
2. Normal copulation	9	9

females after completed copulations with non-foam-producing males. In 18 cloacal fluid samples obtained after completed copulation with a foam-producing male, sperm were observed in 9 (50%).

Foam and fertility.—Fertility in birds can be measured by overall fertility within a certain period, the proportion of females fertilized and, for each female fertilized, the duration of fertility. For an 8-day period after a single copulation, the overall fertility was significantly higher for copulations involving foam, whether natural or artificially placed (45%, 42%, and 40% for treatments 2, 3, and 4, respectively), than copulations without foam (22%) (Table 4).

The proportion of females that laid at least one fertile egg after the copulation in treatments 1, 2, 3, and 4 were 0.1 (4/40), 0.51 (18/35), 0.18 (7/40), and 0.13 (5/40), respectively. Sham-operated males were able to fertilize proportionally more females ($\chi^2 = 9.5$, $P < 0.005$) than cauterized males regardless of timing of artificial placement of foam.

For copulations that involved foam, either natural or artificially placed (treatments 2, 3, and 4), fertility lasted for 7–8 days (Table 4). For copulations without foam (Treatment 1), fertility lasted only 5 days.

Position of the foam in the female after copulation.—During the course of the experiment, we observed that in natural copulations, foam mixed with semen was deposited by intact males in the female proctodeum (Fig. 1). This was confirmed in a separate experiment by injecting a small amount of food color (blue) into the males' proctodeal gland before copulation and sacrificing the females afterwards to examine where the blue foam was deposited and which part of the cloaca was stained (Cheng et al. 1985). Blue foam was found only in the proctodeum of the females, and in no other part of the cloaca or the oviduct. This differs from chickens where the hen everts the distal vagina during copulation and the cock deposits the semen on the exposed portion of the oviduct (Guhl and Fischer 1969).

TABLE 4. Percentage fertility and duration of fertility of eggs laid by females[a] after a single copulation.

Days after copulation	Treatments[b]			
	1	2	3	4
1	0/4[c]	3/14	4/7	1/4
2	3/3	12/14	4/5	4/4
3	1/2	11/15	2/6	3/4
4	0/2	8/14	3/6	2/4
5	1/4	10/16	2/7	0/5
6	0/4	3/17	2/6	3/5
7	0/2	3/14	2/6	1/5
8	0/2	3/13	1/5	0/4
9	0/2	0/11	0/5	0/3
10	0/2	0/13	0/5	0/2
Total (8 days)	5/23	53/117	20/48	14/35
% fertile	22	45	42	40

[a] Females that have laid at least one fertile egg.
[b] 1 = copulation, no foam; 2 = copulation with intact male; 3 = copulation, then foam; 4 = foam, then copulation.
[c] Number of fertile eggs/number of eggs set.

DISCUSSION

We found that in natural copulation, foam affected fertility in three ways. First, the presence of foam, whether placed artificially or naturally, extended the duration of fertility of those females fertilized. Second, in copulations without foam, or with artificially placed foam, the proportion of females fertilized decreased significantly compared with the proportion fertilized in copulations by intact males where foam was placed naturally. The position of the foam deposition, and the mixing of semen and foam during copulation, seemed to be important. Third, the difference in fertility between foam-producing and non-foam-producing males was not because of difference in frequency of sperm transfer. The data were also consistent with the observations that in domestic Japanese Quail, only about 50% of observed completed copulations involved sperm transfer (Adkins 1974).

Ogawa et al. (1974) found that fertility of males whose proctodeal glands were removed surgically was 14.6% compared with 56.5% for controls. Ikeda and Taji (1954) assumed that the foam was part of the seminal fluid, but Lepore and Marks (1966) and Kobayashi et al. (1972)

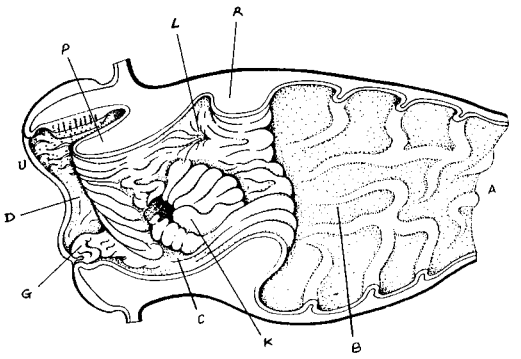

Fig. 1. Cloaca of mature hen: view from the right side. (From Komarek [1971], courtesy of Acta Veterinaria Brno.) (A) rectum; (B) coprodeum; (C) urodeum; (D) proctodeum; (G) clitoris; (K) left oviduct (functional) opens on a rosette-like mound; (L) the ostium of the left ureter; (P) uroproctodeal fold (*plica proctodeourodealis*); (R) coprourodeal fold (*plica urodeocoprodealis*); (U) cloacal opening. Cloaca of mature female Japanese Quail would be similar.

demonstrated that in artificial insemination, where semen was placed in the vagina without foam, the same fertility level was achieved as when semen and foam were mixed.

Without foam, copulation frequency affected fertility. In natural copulations, both fertility and hatchability of fertile eggs was affected adversely by the lack of foam. This indicates that sperm stored in the sperm storage tubules of the females were aged and stale (Nalbandov and Card 1943, Friess et al. 1978). Because foam affected both the proportion of females fertilized and fertility duration, this implies that for copulations by non-foam-producing males, inadequate fresh sperm reached the sperm storage tubules of the females (Van Wambeke 1984). This is consistent with the suggestion (Ikeda and Taji 1954) that foam is a medium for sperm transfer along the oviduct.

We have no explanation for the observation that cauterized UBC-A males exhibited higher mating frequency than intact males of the same genotype, and why this was not observed in UBC-W males. These observations are interesting and deserve to be studied further, but they are not relevant to the role of foam in fertility.

It is possible that the proctodeal gland has developed to play a much more important role in fertilization under domestication where presumably the pressure for fertilizing more females has intensified (Clayton 1972, Haase and Donham 1980). Wild *Coturnix* are mostly monogamous (Wetherbee 1961, Moreau and Wayre 1968, Nichols in prep.). Schleidt and Shalter (1972) reported that the size of the proctodeal glands from captured wild males maintained in the laboratory was much smaller than in domestic strains maintained under identical conditions. The amount of foam that can be squeezed from a wild male's gland was small compared with that obtainable from a domestic male. Similar observations were made by Cheng (unpubl. data) on captive feral Japanese Quail from Hawaii and their captive-reared progeny. Under domestication and with high-density rearing conditions, pair bonds break down and males become promiscuous. Domestic males have the opportunity to fertilize many more females but at the same time face intense competition from other males to fertilize these females (Cheng and Burns 1988). Under these circumstances, the foam gland may enlarge.

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REVIEWERS FOR *THE AUK*, 1988

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