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FOAM PRODUCED BY MALE *COTURNIX* QUAIL: WHAT IS ITS FUNCTION?

ELIZABETH ADKINS-REGAN[1]

Department of Psychology and Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA

ABSTRACT.—Males of the Old World quail genus *Coturnix* are unique among birds in possessing a well-developed proctodeal gland. The gland and associated cloacal musculature are sexually dimorphic, androgen dependent, and produce a foamy substance that is introduced into the female along with semen during copulation, suggesting that the foam plays some role in increasing male reproductive success. I experimentally tested three hypotheses about the function of this foam in Japanese Quail (*Coturnix japonica*): (1) foam functions in sperm competition, (2) foam reduces the female's receptivity to a second male, and (3) foam increases the probability of fertilization when a hard-shelled egg is present in the uterus (hypothesis 3 was originally proposed by Cheng et al. 1989a). Insemination shortly before oviposition fertilized fewer eggs than inseminations earlier in the day, but only if males had a reduced foam complement, supporting the third hypothesis. The other two hypotheses were not supported. Copulation reduced female receptivity, but this effect was not due to the male's foam. *Received 2 February 1998, accepted 22 June 1998.*

IN MOST AVIAN SPECIES, males either have no phallus or have a rudimentary non-intromittent phallus (Briskie and Montgomerie 1997). Thus, mating is accomplished without the elaborate genitalia characteristic of many mammals, reptiles, and insects. Recent interest has developed regarding the possibility that birds have evolved special anatomical and physiological mechanisms to manipulate fertilization, specifically sperm competition or female sperm manipulation (Birkhead and Møller 1992).

Males of the Old World quail genus *Coturnix* are unique among birds in possessing a well-developed proctodeal gland (McFarland et al. 1968, Klemm et al. 1973, Siopes and Wilson 1975, Bakst and Cecil 1985). In domesticated Japanese Quail (*Coturnix japonica*), a large, red protuberance is present immediately dorsal to the cloacal opening (Fig. 1). This protuberance, the foam gland complex, is distinctly different from the cloacal protuberances of some passerines (it does not contain the coiled vas deferens) and is not a sperm-storage organ. It consists of an enlargement of the dorsal portion of the sphincter cloacae muscle plus the proctodeal gland proper, the units of which are interdigitated with sphincter cloacae muscle fibers (Klemm et al. 1973). The proctodeal gland secretes a viscous mucoprotein that is then "whipped" into foam by the action of the sphincter cloacae (Ikeda and Tajii 1954, Fujii and Tamura 1967, Seiwert and Adkins-Regan 1998). The foam gland complex is markedly sexually dimorphic (large in males but rudimentary in females), is well developed in males only during the breeding season, and is highly androgen dependent (Nagra et al. 1959, Beach and Inman 1965, Sachs 1967, Adkins and Adler 1972, Siopes and Wilson 1975).

During copulation, the male introduces not only semen but also a large quantity of foam into the female. The rhythmic movements of the sphincter cloacae that are known to "whip up" the foam increase greatly in frequency as soon as the male detects the female, in advance of actual mounting and cloacal contact (Seiwert and Adkins-Regan 1998). These observations suggest that the foam functions to increase the male's reproductive success by promoting fertilization (Ogawa et al. 1974, Fujihara 1992).

Female Japanese Quail are unusual in that they lay eggs in the late afternoon (Wilson and Huang 1962) rather than in the morning as in many other bird species (Skutch 1952). Females also are more sexually receptive behaviorally in the afternoon (Delville et al. 1986). Cheng et al. (1989a, b) proposed that foam enabled a male to fertilize a female even when a hard-shelled egg was in the uterus during mating, which would often be the case for matings oc-

[1] E-mail: er12@cornell.edu

FIG. 1. External view of the foam gland complex (feathers removed) of a reproductively active male Japanese Quail. Arrow indicates the cloacal opening. Photograph by Marie Read.

curring in the afternoon during the female's peak of receptivity. In support of this hypothesis, Cheng et al. (1989a, b) reported that foam prolonged sperm motility *in vitro* and that male Japanese Quail whose foam glands had been destroyed by cauterization fertilized few or no eggs.

Cauterization is a potentially confounding manipulation, however, because the interdigitation between the proctodeal gland and the sphincter cloacae muscle makes it impossible to destroy the gland without damaging this muscle. Because the sphincter cloacae is essential for copulation (i.e. for cloacal contact and

ejaculation; King 1981, Seiwert and Adkins-Regan 1998), it is likely that cauterized males are defective in components of copulation critical for fertilization success other than foam production. Also, neither *in vitro* observations nor cauterization experiments provide a direct test of the hypothesis that foam increases fertilization success mainly when a hard-shelled egg is present.

The experiments reported here use a less invasive manipulation to test the above hypothesis and also test two additional hypotheses for the function of foam. One is that foam enables a male to reduce the ability of a second male to fertilize the female; that is, that it functions in sperm competition. Foam could function as a mechanical device analogous to the sperm plugs of some other vertebrates, or it could act chemically, for example, by enabling a male's sperm to remain motile longer than a competing male's sperm. The second hypothesis is that the foam reduces the female's receptivity (again decreasing the likelihood that a second male would be able to fertilize the eggs), but through a different mechanism, the female's behavior. Both of these hypotheses assume that females might mate with multiple males. Although little is known about the mating system of wild Japanese Quail, extrapair copulations have been observed in feral Japanese Quail in a seminatural environment (Nichols 1991), and field observations of the closely related Common Quail (*Coturnix coturnix*) suggest that situations in which females switch mates, or in which more than one male attempts to copulate with a female, occur rather frequently (Rodrigo-Rueda et al. 1997).

METHODS

Birds, mating trials, and fertilization measures.—The quail used in this study were hatched from eggs purchased from Truslow Farms, Chestertown, Maryland, and were housed individually after the age of four weeks (sexual maturity begins at ca. five to six weeks). All birds were at least eight weeks old and not more than eight months old during the experiments and were housed on a 16:8 light : dark cycle. A new set of birds was used for each experiment, and males were sexually experienced prior to use.

In this species, ejaculation and insemination occur with the first cloacal contact if the male is competent and the female is receptive. Immediately after ejaculation, the male dismounts and often fluffs his feathers and struts. The entire sequence lasts only a few seconds. If the male is less competent or the female is unreceptive, repeated chasing, mounting, and attempted cloacal contact occur, which sometimes but not always results in successful ejaculation and insemination. Foam is deposited in the female's proctodeum (Cheng et al. 1989a), and sperm are not found in the female unless foam is also present (Adkins 1974). Thus, insemination can be confirmed by examination of the female (the foam is clearly visible in the proctodeum) or, if tactile contact with the female's cloaca might introduce an experimental confound, by close observation of the male's behavior (cloacal contact followed by sudden cessation of the copulatory attempt followed by feather fluffing and/or strutting). For data validating the use of the male's behavior to judge successful insemination, see Adkins-Regan (1995).

Depending on the experiment, females were allowed to copulate with a male either in their home cages (21 × 18 × 15 cm hardware cloth), a small testing cage (38 × 24 × 18 cm), or a large testing cage (183 × 91 × 77 cm). Cage size has no effect on the likelihood that an insemination will fertilize eggs or on the number of eggs fertilized (Adkins-Regan 1995). If the male did not begin copulating immediately, he was replaced with another male. The male was removed after insemination, and except when measuring female receptivity, only results from mating trials in which the male achieved insemination were analyzed. Unless stated otherwise, mating trials were conducted between 1130 and 1500 EST, a time when females are likely to be receptive.

Most eggs were laid between 1600 and 2000. Eggs were collected daily in the morning (beginning the morning after mating) for 11 days, which is the maximum sperm-storage interval in this species and in birds in this laboratory (Sittman and Abplanalp 1965, Adkins-Regan 1995). Eggs were stored at 13°C for a maximum of two weeks prior to incubation at 38°C and 60% relative humidity. Eggs were broken open after one week of incubation and recorded as fertile if any embryonic development had begun. It is possible for eggs to be fertilized, in the sense that sperm are attached to the outer perivitelline layer, without any embryonic development being initiated (Birkhead et al. 1994). Such outcomes do not, however, contribute to a male's reproductive success. Therefore, because my experiments test hypotheses about how foam influences male reproductive success, all eggs with no embryonic development were categorized as infertile, and "successfully fertilized" should be taken to mean fertilized such that embryonic development takes place. Early embryonic deaths occurred at a low rate (in each experiment constituting 6% or less of all eggs recorded as fertile) and were unrelated to experimental condition. They were recorded as fertile eggs, but results are not different if these eggs are excluded from analysis. Data from poor layers (i.e. females that laid fewer than five

unbroken hard-shelled eggs in the 11 days following the mating trial) were excluded from analysis.

Egg fertility data were analyzed by nonparametric statistics (χ^2 or Mann-Whitney *U*-tests) because the distribution of outcomes is bimodal (Adkins-Regan 1995); about one-third of inseminations do not fertilize any eggs. In analyzing numbers and percentages of fertile eggs, trials using the same male or female were considered statistically independent. In prior work from our laboratory, trials were conducted using several different cohorts of quail over a period of several years (Adkins-Regan 1995), and fertilization outcomes using the same male or female were uncorrelated. Only if both the male and the female were the same (which was not the case in any experiment reported here) were the outcomes correlated. All *P*-values are two-tailed.

Hypothesis 1: Foam is a sperm competition device.—This hypothesis was tested by introducing foam into a female's proctodeum and determining its effect on a male's ability to fertilize her eggs. Males in this case will be referred to as "target" males. Two procedures were used to introduce foam into the females. One was to pair the female with a male housed on a short photoperiod (8:16 light : dark cycle) and receiving androgen replacement (daily injection with 0.5 mg testosterone propionate plus 0.5 mg dihydrotestosterone propionate dissolved in sesame oil). Such males have a developed foam gland complex, produce a normal amount of foam, and copulate, but they have regressed testes and produce no sperm. I refer to these males as "foam donors." Forty females were allowed to copulate with one of 20 target males and 9 foam donors in the small testing cage so as to yield four kinds of mating trials: (1) foam donor immediately followed by target male, (2) target male immediately followed by foam donor, (3) target male only, and (4) foam donor only. Trials of type 4 were included to confirm that the donors introduced foam into females but could not fertilize any eggs. Successful insemination was judged by observation of the male's behavior and, for trials of type 4, by successful foam donation as confirmed by examination of the female's proctodeum.

The second procedure for introducing foam into females was to express foam from one of 20 normal fertile males, place it in a 5-cc plastic, blunt-tipped syringe, and inject the foam into the female's proctodeum. Twenty-nine females and 10 males were allowed to copulate in the female's home cage to yield two kinds of mating trials: (1) experimental trials in which foam was introduced into the female via a syringe immediately before mating, and (2) control trials in which the tip of the empty syringe was introduced into the female's proctodeum for 2 s immediately before mating. Alternate females were assigned to the experimental and control trials. Two weeks later the females were allowed to copulate again, reversing the trial assignments. Successful insemination was judged by observation of the target male's behavior.

Hypothesis 2: Foam reduces female receptivity.—In two experiments, similar procedures for introducing foam into a female as described above (foam-donor males and syringed foam) were used to determine the effect of foam on a female's receptivity with a target male. In both experiments, 21 females were paired with the same target male (thus, 21 target males) on four consecutive days. The same target male was used for a given female to reduce day-to-day variation in a female's behavior toward a target male. These tests took place in the large testing cage to allow the female to run or fly from the male. On two of the four days the female was tested without any prior manipulation, on one day the female received foam (via a male donor or via syringe) prior to the test with the target male, and on one day the female received a control manipulation prior to the test with the target male. The order of the tests was counterbalanced.

In the first experiment, females received foam prior to testing by copulating in their home cages with foam donors who had the normal complement of foam in the foam gland complex; the test with the target male began one minute after the donor finished copulating. Because behavior (receptivity) was the dependent variable rather than egg fertilization success, foam-donor males did not need to be infertile and so were untreated males housed on long days. For the control manipulation, the females also copulated in their home cages and were tested with the target male one minute later, but the home-cage copulations were with donor males whose foam had been manually expressed immediately prior to mating. Manual expression greatly reduces the amount of foam that the donor places in the female; if females copulate immediately following manual expression of foam, no foam can then be seen in the female's proctodeum. This manipulation thus controls for effects of copulation on subsequent receptivity that are due to factors other than foam, such as tactile stimulation from cloacal contact itself. In the second experiment, foam from two donor males was introduced into the proctodeum via syringe, and the test with the target male began one minute later. For the control manipulation, the empty syringe was introduced. For both experiments in the tests with the target male, receptivity was scored on a four-point system: 0 = highly unreceptive, constantly moves away from male; 1 = unreceptive but not markedly so; 2 = ambiguous receptivity; and 3 = clearly receptive, squats and does not move while mounted. If the female's receptivity status changed during the copulation attempt, the mean of the initial and final scores was used. The number of times the female ran from the male or took flight during the test was also recorded. For analysis, the mean of the two target-only

tests was compared with each of the other two kinds of tests. Results were analyzed by sign tests.

Hypothesis 3: Foam increases fertilization when a hard-shelled egg is present.—Fifty-eight females copulated with 25 males such that each male copulated twice on consecutive days, once with the normal complement of foam and once immediately following manual expression of foam. Order of male conditions (foam vs. reduced foam) was counterbalanced. Copulations occurred between 0830 and 1800, with most occurring before 1400. Successful insemination was judged from the male's behavior. The experiment was then repeated with a new set of birds (53 females and 22 males) but with all copulations conducted between 1800 and 1900, shortly before but prior to expected oviposition. Cages were checked for egg production between 1800 and 2000 and then again the next morning, and those few trials without subsequent oviposition were eliminated from analysis. Eggs found the morning following mating were noted but were not incubated for fertilization determination because these eggs are never fertilized (Adkins-Regan 1995).

In order to obtain additional information about how quickly a male can regenerate a normal complement of foam following manual expression of the contents of the foam gland complex, manual expression was performed on five additional males (seven months old) twice daily for six days such that the first and second expressions (time 1 and time 2) were 2.5, 5, 10, 20, or 40 min apart. The order of time intervals for the different males was counterbalanced across days, and time 1 was at the same time of day for all males. Expressed foam was weighed to the nearest mg and the difference was determined between the weights produced at times 1 and 2 on each day. Data were analyzed by an analysis of variance for repeated samples followed by post-hoc *t*-tests with a Bonferroni correction.

RESULTS

Experiments testing whether foam is a sperm competition device.—The results of the first experiment, in which foam was introduced into females by donor males housed on short days, are shown in Table 1. Copulations with foam donors only, as expected, fertilized no eggs. There were no effects of the foam donor on the egg fertilization success of target males. When foam donor + target trials were compared with target-only trials, no significant differences occurred in the percent with a fertile egg (χ^2 = 0.8, df = 1, $P > 0.3$) or in the median percent of eggs fertile (including trials yielding no fertile egg, Mann-Whitney $U = 114$, $P = 0.17$; excluding trials yielding no fertile egg, $U = 55.5$, $P = 0.28$). This was also the case when target + foam donor trials were compared with target only trials (% trials with a fertile egg, $\chi^2 < 0.001$, df = 1, $P > 0.9$; median % eggs fertile including trials yielding no fertile egg, $U = 119$, $P > 0.5$; median % eggs fertile excluding trials yielding no fertile egg, $U = 67$, $P = 0.30$). When eggs laid the day after mating, which are the first eggs that could possibly be fertile, were analyzed separately (excluding trials with no fertile egg), again no significant differences occurred between donor + target and target alone trials (85 vs. 87% fertile, $\chi^2 = 0.02$, df = 1, $P > 0.8$) or target + donor and target alone trials (100 vs. 87% fertile, $\chi^2 = 0.88$, df = 1, $P > 0.3$). Using the alternative procedure of placing foam in females via syringe (Table 1), again there was no effect of the foam on the ability of target males to fertilize females, i.e. no significant difference between foam + target and syringe + target (control) trials (% trials with a fertile egg, $\chi^2 = 0.39$, df = 1, $P > 0.5$; median % eggs fertile including trials yielding no fertile egg, $U = 233$, $P = 0.057$; median % eggs fertile excluding trials yielding no fertile egg, $U = 168$, $P = 0.1$). Even if foam + target and syringe + target outcomes are compared with Wilcoxon matched-pairs tests, the differences are not significant (all Ps > 0.1).

TABLE 1. Test of the hypothesis that foam is a sperm competition device in Japanese Quail based on foam-donor males and based on syringed foam.

Type of mating	No. of trials	% Trails with fertile egg	Median % eggs fertile[a]
Foam-donor males			
Foam donor + target	13	77	50 (57)
Target + foam donor	11	64	20 (40)
Target only	24	63	33 (50)
Foam donor only	8	0	0
Syringed foam			
Foam + target	24	79	29 (33)
Syringe + target	28	89	40 (40)

[a] Values in parentheses exclude trials that yielded no fertile eggs.

Experiments testing whether foam reduces female receptivity.—Copulating with a foam versus a no-foam male prior to testing with a target male had no significant effect on receptivity or on running and flying behavior by females (sign tests; foam male vs. no male, $P = 0.34$; run + fly following foam male vs. no male, $P =$

0.77; no-foam male vs. no male, $P = 0.11$; run + fly following no-foam male vs. no male, $P = 0.39$). Nor did the female's behavior with target males differ as a function of whether the first (donor) male had a normal complement of foam (foam vs. no-foam male, $P = 0.18$; run + fly following foam vs. no-foam male, $P = 0.75$). When these two kinds of tests (foam male and no-foam male) were combined for analysis by taking the mean of the two tests, it was evident that females were less receptive when there had been a prior male (see Fig. 2A). Thus, copulating with one male reduced a female's receptivity to a subsequent male, but this reduction was not due to the first male's foam. In the second experiment (Fig. 2B), most differences between test types were not significant (sign test, Ps > 0.3). Females tended to run and fly more when foam had been introduced via syringe prior to testing, but the difference between these tests and tests with no syringe was not significant ($P = 0.076$). When syringe + foam and syringe tests were combined (by taking their means) and compared with no syringe tests, it was evident that the introduction of a syringe into the female increased her tendency to run and fly in the presence of the target male (Fig. 2B), but again this effect was not due to the presence of foam.

Experiments testing whether foam increases fertilization in the presence of a hard-shelled egg.— Across all trials, fertilization success of trials conducted at the two times of day (1800 to 1900 vs. 0830 to 1800) did not differ (% of trials producing any fertile eggs, 47 vs. 61%, $\chi^2 = 1.72$, df = 1, $P > 0.1$; % eggs fertile including trials yielding no fertile eggs, $U = 1{,}227$, $P = 0.076$; % eggs fertile excluding trials yielding no fertile eggs, $U = 560$, $P = 0.19$). Successful fertilization was possible even shortly before oviposition. For example, one female oviposited 5 min after mating, yet 50% of her subsequent eggs were fertilized. Across all trials, fertilization success was lower with a reduced foam complement (40% of trials with reduced foam vs. 70% of trials with normal foam produced at least one fertile egg; $\chi^2 = 9.44$, $P < 0.01$; % eggs fertile including trials yielding no fertile eggs, $U = 1{,}170$, $P = 0.032$; % eggs fertile excluding trials yielding no fertile eggs, $U = 398$, $P = 0.40$). This negative effect of reduced foam on egg fertilization was most pronounced for trials conducted between 1800 and 1900, shortly before oviposition. When the two mating times were analyzed separately, the difference between normal and reduced foam trials was significant for 1800 to 1900 but not for 0800 to 1800 (Table 2, Fig. 3). Thus, reduced foam affected the outcome mainly at the time when a greater number of females would have had a hard-shelled egg in the uterus. This effect was not specific to the first potentially fertilizable egg

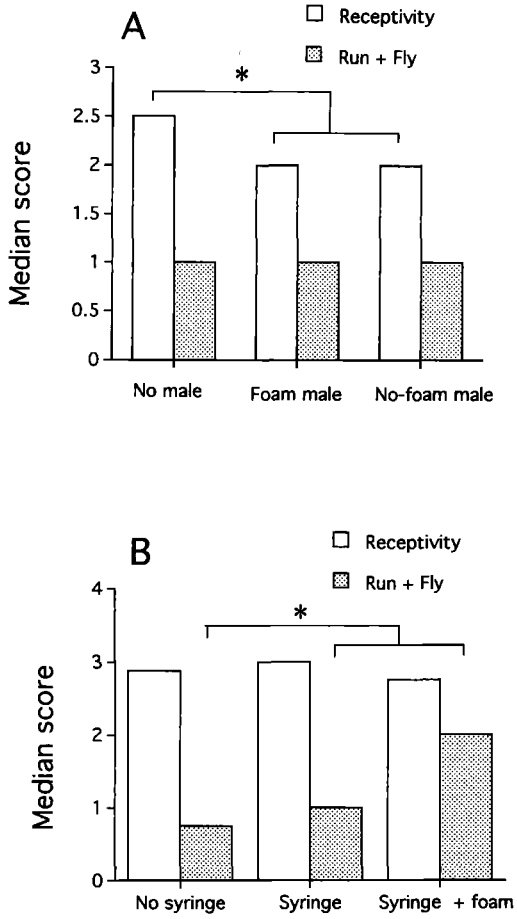

FIG. 2. (A) Female behavior with a target male after mating with a male with normal foam (foam male), a male whose foam has been manually expressed (no-foam male), or no prior male. (B) Female behavior with a target male after introduction of foam into the female's proctodeum via syringe (syringe + foam), introduction of empty syringe (syringe), or no prior manipulation (no syringe). *, $P < 0.05$ when the two conditions indicated are combined and compared with no male tests (A: sign test, $P = 0.012$) or with no syringe tests (B: sign test, $P = 0.036$).

TABLE 2. Test of the hypothesis that foam increases fertilization when a hard-shelled egg is present in the oviduct of female Japanese Quail.

Type of mating	Time of day	No. of trials	Median % eggs fertile[a]
Normal foam	1800 to 1900	25	22 (44)
Reduced foam	1800 to 1900	30	0 (50)[b]
Normal foam	0800 to 1800	29	33 (50)
Reduced foam	0800 to 1800	28	26 (50)

[a] Values in parentheses exclude trials that yielded no fertile eggs.
[b] Mann-Whitney $U = 507$, $P = 0.032$ compared with normal foam matings at 1800 to 1900. See Figure 3 for the percentage of trials with a fertile egg.

following mating. When eggs laid the afternoon of the day after mating (i.e. the first eggs that could have been fertilized) were analyzed separately for matings conducted between 1800 and 1900, fertilization success tended to be lower with reduced foam (25% fertilized with reduced foam vs. 43% with normal foam), but in contrast to the analysis of all eggs, this difference was not significant ($\chi^2 = 1.02$, df = 1, $P > 0.3$).

The results of the experiment determining how quickly males generate a normal foam complement following manual expression of foam are shown in Figure 4. Most males had fully regenerated their foam complement by 40 min, but very few had done so before 10 min (Fig. 4). The variability in these data may result not only from individual differences in the speed of foam recovery, but also from whether males had spontaneously released foam shortly before foam was expressed for weighing at time 1, time 2, or both. Males normally deposit a blob of foam on each pile of excreta (Ikeda and Tajii 1954), and they void their excreta frequently.

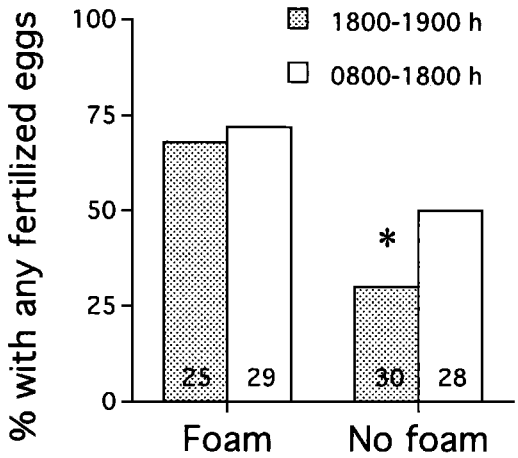

FIG. 3. Test of the hypothesis that foam increases fertilization when a hard-shelled egg is present. Females copulated with males possessing a normal foam complement (foam) or a reduced foam complement (no foam) shortly prior to oviposition (1800 to 1900) or earlier in the day (0830 to 1800). See Table 2 for other measures (*, $\chi^2 = 6.45$, df = 1, $P < 0.02$, compared with normal foam copulations at 1800 to 1900).

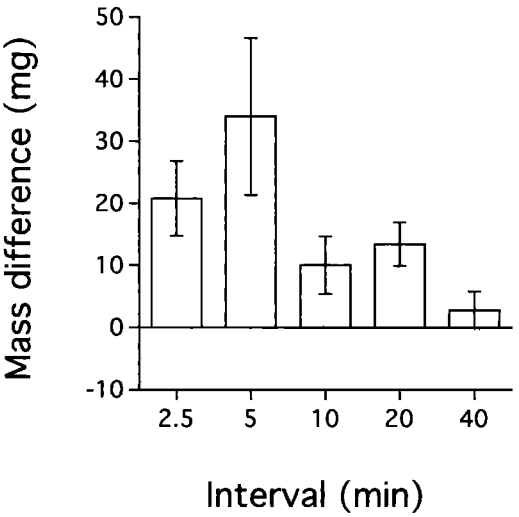

FIG. 4. Foam recovery by males following manual expression. Foam was expressed and weighed at times 1 and 2. The X-axis is the interval between time 1 and time 2, and the Y-axis is the mean ± SE of the mass at time 1 minus the mass at time 2. Thus, a difference of 0 indicates that the male has completely recovered his foam complement, and a difference greater than 0 means that he has not yet recovered his foam complement. The overall effect of time interval was significant ($F = 2.96$, $P = 0.047$). Scores at intervals 5 min and 40 min were significantly different ($P < 0.05$), and scores at interval 40 min were not significantly different from 0 (that is, by 40 min, time 1 and time 2 masses no longer differed, $P < 0.05$).

DISCUSSION

These results provide further evidence that male Japanese Quail can successfully fertilize future eggs even when the female has a hard-shelled egg in the uterus during mating, and they confirm Cheng et al.'s (1989a, b) hypothesis that the male's proctodeal gland foam in-

creases the likelihood of successful fertilization at this time. The experimental manipulation used here, manual expression of foam from the male prior to mating, does not interfere with copulation or with ejaculation of sperm. It does not completely eliminate all foam, but the results of the experiment to determine recovery of a normal foam complement indicate that foam was substantially reduced at the time of mating, immediately after manual expression.

Cheng et al. (1989a, b) implied that a foam gland evolved in male *Coturnix* because of the special problem created by the temporal coincidence between imminent oviposition and maximum sexual receptivity in the female. Although it is not possible based on current information to know which suite of characteristics came first, the male's or the female's, one implication of this scenario is that in species that do not produce foam, successful fertilization at this time would be unlikely even if males could achieve insemination. Fertilization success of artificial insemination of domesticated fowl (*Gallus gallus*), turkeys (*Meleagris gallopavo*), and Muscovy Ducks (*Cairina moschata*) shortly before oviposition is indeed low (Birkhead et al. 1996). It is not clear, however, whether this is the same phenomenon as seen in Japanese Quail mating with a reduced foam complement, for two reasons. First, in the studies discussed by Birkhead et al. (1996), fertilization success was low when insemination occurred shortly after and before oviposition. Second, in those studies the reduction in fertilization success applied mainly to the next potentially fertilizable egg, not to all eggs, in contrast to the present results in which the next potentially fertilizable eggs were not disproportionately affected.

By what mechanism does foam aid fertilization in male Japanese Quail? The foam has interesting physical and chemical properties, either of which could be involved in buffering sperm during oviposition. The foam is a viscous fluid consisting of mucopolysaccharides and/or mucoproteins (Fujii and Tamura 1967, Klemm et al. 1973) into which bubbles of air are whipped by the action of the sphincter cloacae muscle (Seiwert and Adkins-Regan 1998). Its foamy consistency is quite stable, at least outside of the animal (pers. obs.). Foam prolongs sperm motility *in vitro* (Cheng et al. 1989b). Japanese Quail, like many other birds, have sperm-storage tubules (SSTs) at the uterovaginal junction and also at the infundibulum in the upper oviduct, the site of ovum fertilization (Lake 1975, Friess et al. 1978, Hatch 1983, Shugart 1988, Bakst 1993b, Birkhead and Fletcher 1994). If oviposition occurs before the sperm have reached the SSTs, foam might help the sperm remain motile until the egg has passed and they can resume their journey to the tubules, or it might help prevent the sperm from sticking to the egg shell or in some other way being displaced and prevented from entering the SSTs (Cheng et al. 1989b; Bakst 1993a, b). Foam manipulation affected the percentage of trials yielding fertile eggs but not the percentage of eggs fertilized if any were fertilized (Table 2, Fig. 3). Furthermore, the first potentially fertilizable eggs were not disproportionately affected by the foam manipulation. Taken together, these findings suggest that foam influences whether sperm reach the SSTs in sufficient numbers to be used at all, rather than how quickly they reach the SSTs.

The other two hypotheses of foam function were not supported. Foam from one male did not reduce the fertilization success of a second male. Copulating with one male reduced subsequent receptivity toward a second male somewhat, but this effect was not due to the male's foam. Exactly how long a female's receptivity is reduced following copulation has not been determined, although it is clear that receptivity is fully recovered by the following day. Reduction or termination of female receptivity following copulation is a widespread phenomenon (Greenberg and Noble 1944, Adler and Allen 1983, Whittier and Tokarz 1992, Erskine 1995). Receptivity in domesticated turkeys has been shown to be caused by eversion of the oviduct in response to tactile stimuli (Schein and Hale 1965). Its function has usually been assumed to be the same as mate guarding by males, but this does not address the question of why females should reduce their receptivity following copulation, especially females that mate multiple times. An alternative explanation is that reduced receptivity is a mechanism whereby females control sperm usage by, for example, letting the first male's sperm reach the SSTs before interference from a second male can occur, or by preventing one male from copulating twice in close succession and thus filling all of the SSTs. Observations of wild

Common Quail and feral captive Japanese Quail suggest that mate switching and extra-pair copulations do occur (Nichols 1991, Rodrigo-Rueda et al. 1997). Although the foam itself does not seem to function as a sperm competition device, other opportunities for sperm competition are likely to occur in this species. Such opportunities conceivably could occur even during the immediate postcopulatory period, because male Japanese Quail engage in forced copulations with unreceptive females. These forced copulations, although less successful at achieving inseminations than other copulations, have the same fertilization success as other copulations if insemination is achieved (Adkins-Regan 1995). In other words, the female's efforts to control sperm usage might not always be successful. The testis size of male Japanese Quail also suggests that considerable sperm competition occurs in this species.

The hypotheses tested here do not exhaust the possible functions of foam in male Japanese Quail. Each pile of excreta of a breeding male has a blob of white foam on top; these piles are deposited throughout the day as the male moves about. A domesticated male housed in the laboratory deposits about 1.5 g of foam per day on its excreta (Adkins-Regan unpubl. data), which could entail some physiological cost. Schleidt and Shalter (1972) suggested that foam functions in territory maintenance by visually marking the male's area. Although more recent observations cast doubt on the idea that *Coturnix* are territorial (Nichols 1991, Rodrigo-Rueda et al. 1997), a signaling function of the male's foam cannot be ruled out at this time.

Although the foam gland in Japanese Quail is highly sexually dimorphic, androgen dependent, and increases fertilization success when oviposition is imminent, little evidence exists to suggest that sexual selection has played a role in its evolution. The existing observations of mating behavior suggest the potential for sexual selection in this species, however, which may have played a role in the evolution of two other striking male characters: crowing and testis size. Females are attracted to playbacks of the male's crow, which is a loud sexually dimorphic signal given frequently during the breeding season (Goodson and Adkins-Regan 1997), and male *Coturnix* have relatively large testes for their body size compared with other birds (Møller 1991).

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