

DOMINANCE RELATIONSHIP AND MATING BEHAVIOR OF DOMESTIC COCKS—A MODEL TO STUDY MATE-GUARDING AND SPERM COMPETITION IN BIRDS¹

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Abstract. A random-bred strain of domestic chickens (*Gallus gallus*) in single-male and two-male mating groups was used as a model to study strategies of mate guarding and sperm competition. The experiment was designed to examine influences of (a) the presence of a rival male, (b) dominance status of the males in the two-male groups, and (c) the time of day on the frequencies of male courtship and copulations. In the absence of rivalry, male chickens copulated infrequently in the morning and increased the frequency of copulations throughout the day until a maximum was reached in late afternoon. In the two-male groups the dominant males copulated more frequently than the subordinate males. They also competed by altering their diurnal pattern of mounting attempts and increasing their rate of successful copulation per attempt. The subordinate males made frequent attempts to mount the females regardless of whether they were receptive. However, their success rate was low because of interference by the dominant males, especially at that time of the day when a successful insemination would likely fertilize eggs. The experiment showed that not only the relative numbers of copulations by different males, but also the timing and success of copulations by different males may influence the probability of paternity. Furthermore, the interplay of proximate mechanisms and evolutionary factors contributed to variations in mating strategies.

Key words: Chickens; mate guarding; diurnal pattern; dominance; sperm competition; animal model.

INTRODUCTION

Extra-pair copulations (EPC) have been observed in many apparently monogamous bird species (McKinney et al. 1984), and multiple paternity of clutches has been shown to occur in some of these species (Burns et al. 1980, Gowaty and Karlin 1984, Westneat 1987, Evarts and Williams 1987). In domesticated birds, pair bonding usually breaks down and a tendency to promiscuity develops. In the absence of other selective forces such as predation and starvation, and with high density rearing, competition among males for mating is intensified (Clayton 1972). Although such conditions may not be apparent in some domestic birds such as parrots and pas-

serines (Sossinka 1982), it is certainly true for most poultry species. Therefore, it is expected that strategies for sperm competition are enhanced in some domestic birds. Furthermore, related behavior is easier to observe in domestic than in wild birds. With these considerations in mind, we decided to try to use domestic birds as models to study competition strategies and then determine if these strategies or their variants are also adopted in natural populations.

In feral chickens (*Gallus gallus*), most hens mated with the dominant territorial males (McBride et al. 1969). In domestic chickens, males low in the peck order mated infrequently or not at all, whereas the dominant male sired about 65% of the progeny produced by the flock (Guhl et al. 1945, Guhl and Warren 1946, Craig and Bhagwat 1974). Birkhead (in press) listed four factors that would influence the probability of paternity in competitive situations: (1) the timing and success of copulation by different males,

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(2) the relative numbers of copulations by different males, (3) the duration of sperm storage, and (4) sperm precedence. The experiment reported here examines strategies (timing and frequency of copulation) employed by the males of a random-bred strain for competition to fertilize eggs. An inbred strain was also included in the design mainly for obtaining information for a concurrent study (Cheng et al. 1984). Nevertheless, inbred chickens were known to be less competitive socially (Craig and Baruth 1965) and a comparison of the random-bred and the inbred strain may also yield interesting insights.

MATERIALS AND METHODS

We used the random-bred Minnesota Marker (MM) strain that was established from crossing eight different breeds of chickens (Shoffner 1972) and had been maintained as a random-bred population closed to further immigration for the last 10 generations prior to this experiment. The other strain was the Minnesota 420 (I-420), an inbred line of single comb white leghorn. The line was started in 1937 through full- and half-sib matings (Shoffner et al. 1953), and the coefficient of inbreeding for the population was above 90% at the start of the experiment.

Birds used in this experiment were approximately 1 year old and had previous breeding experience. Although the two strains were not raised as an intermingled flock, they were housed in adjacent pens or cages so that they had visual contact with each other. Only laying females were used in the experiment. The experimental design has been described in detail by Cheng et al. (1984). Briefly, there were two replications and each replication consisted of the following eight treatment groups: 1: One I-420 male with four I-420 females; 2: Two I-420 males with four I-420 females; 3: One MM male with four I-420 females; 4: Two MM males with four I-420 females; 5: One I-420 male with four MM females; 6: Two I-420 males with four MM females; 7: One MM male with four MM females; and 8: Two MM males with four MM females.

Each group was placed in a 2.5 m × 2.5 m indoor pen with wood-shaving litter. The sides of each pen were covered with asphalt roofing material 61 cm high to act as a visual barrier. The birds were exposed to a 14L:10D lighting scheme (lights on 08:30 to 22:30) with water and feed provided ad libitum. Observations started 2 days after the birds were placed in the pens. During

the next 14 days, five 30-min observations were made on each group during each of the four time periods: Morning I: 09:00 to 09:59; Morning II: 10:00 to 10:59; Afternoon I: 19:00 to 19:59; and Afternoon II: 20:00 to 20:59. A total of 20 observations (10 hr) was made on each group.

During the observation periods, all male-male and male-female interactions were recorded; in particular, the frequencies of the following components of mating behavior.

Approaching: male approaching female with head oriented towards her.

Precopulatory waltzing (Guhl and Fischer 1969): male waltzing before, or without, mounting attempt. Waltzing is a courtship display (Krujtit 1966).

Crouching: female crouching (receptive posture) before male attempts to mount. In response to the males' approach or waltzing, a hen may also avoid by stepping aside or escape by running, showing her unwillingness to copulate.

Mounting attempt: male grasping female by the back of the head and attempting to mount (at least one foot on female's back).

Successful mounting attempt: male has both feet on female's back.

Treading: male treads with both feet in a treadmill fashion on female's back.

Tail bending: male bending his tail around the side of the female's tail. Tail bending was considered an indicator of completed copulation.

At the end of the 2-week period, a new set of birds was put in the pens and the experiment was repeated after the new birds were allowed 2 days for habituation.

When unacquainted chickens are put together, dominance-subordinate relationships soon develop by agonistic interactions (Guhl and Fischer 1969). Males dominate females but males and females have separate peck orders. Agonistic behavior includes attack (fighting, pecking, and threatening), escape, avoiding, and submissive behavior. These patterns of activity can easily be recognized by differences in posture and movement. In each two-male mating group, the male who won more of the agonistic encounters was designated dominant and the other as subordinate. In all cases, dominance relationships were established before the start of the observation period and remained stable throughout the ex-

TABLE 1. Relationship of strain (MM = Minnesota Marker; I-420 = Minnesota 420) and dominance of male chickens to mating behavior.

Strain and dominance	Male mating behavior†			
	Mounting attempts	Successful mounting	Treading	Tail bending
MM				
Dominant	4.9	2.19*	1.94*	1.44**
Single	5.2	1.19	0.88	0.75
Subordinate	5.2	0.62	0.38	0.31
I-420				
Dominant	3.5	0.86	0.81	0.56
Single	5.4	1.69	1.19	0.50
Subordinate	2.2	0.58	0.00**	0.00*

† Frequency per male per five observations (2.5 hr).
* $P < 0.05$. ** $P < 0.01$; significant differences from single males of their own strain.

periment. There were no cases in which it was difficult to determine which male was dominant. Males in one-male mating groups are referred to as the single males.

The cumulative frequencies of the seven components of mating behavior measured were analyzed separately by analysis of variance with repeated measures (Snedecor and Cochran 1980). The statistical model has been described in Cheng et al. (1984). The independent variables were replication, male genotype, female genotype, male status (single, dominant, or subordinate), and time of observation. All the two-way and three-way interactions involving the main effects were examined. Since in the two-male mating groups both dominant and subordinate males were interacting with the same six females, data collected from one male were not independent from those collected from the other male. The mating behavior of the dominant males and the subordinate males were therefore also compared statistically with that of the single males (control) in separate analyses to overcome this problem.

The analyses were conducted with the aid of a computer program, "IVAN" (Weisberg and

TABLE 2. The temporal pattern of mounting attempts between dominant and single males.

Male status	Mean frequency of mounting attempts†			
	Morning I	Morning II	Afternoon I	Afternoon II
Dominant	4.6c	1.5a	4.1bc	6.6d
Single	2.8ab	3.6b	5.6cd	9.4e

† Per male per five observations. Means followed by different letters were significantly different ($P < 0.05$).

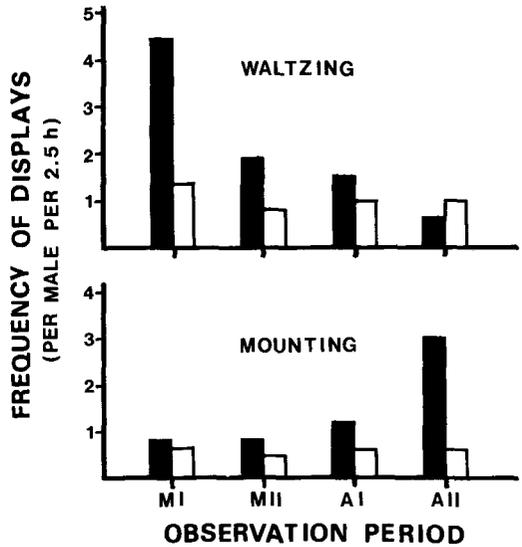


FIGURE 1. Difference in the diurnal pattern of precopulatory waltzing and successful mountings between subordinate (open bars) and single (black bars) males observed during the morning (MI and MII) and afternoon (AI and AII) periods.

Koehler 1979), at the University of Minnesota Computer Center. Square-root transformation was applied to crouching, treading, and tail bending, the three variables with low frequency of occurrence, before the analyses. χ^2 analyses were also used to test differences in ratios or proportions (e.g., mating efficiency in terms of tail bendings/mounting attempt).

RESULTS

In both the random-bred and the inbred strains, the dominant male exhibited a higher frequency of successful mounting and copulation than the subordinate male (Table 1). There were no significant differences among the dominant, subordinate, and single males of either strain in their frequencies of approaching females, performing precopulatory waltzes, and mounting attempts. However, there were some interesting differences in the diurnal pattern of these behaviors.

DIFFERENCES IN THE DIURNAL PATTERN IN MATING BEHAVIOR AMONG DOMINANT, SINGLE, AND SUBORDINATE MALES

While the frequency of mounting attempts by single males started low in the early morning period and increased through the later periods until reaching the highest frequency in the late

TABLE 3. Interference in mounting attempts (MA) of subordinates by dominant males in the random-bred (Minnesota Marker) strain.

	Observation periods			
	Morning I	Morning II	Afternoon I	Afternoon II
Total number of MA by subordinates	15	13	20	35
Proportion of MA interfered by dominant males	0.40	0.14	0.25	0.35
Mating efficiency of subordinates (TB/MA)*	0.07	0.08	0.10	0.03

* TB = tail bending. No statistical test was performed because of rare occurrence of events.

afternoon (Table 2), dominant males maintained a relatively high frequency of mounting attempts in the early morning period, and the two afternoon periods while making very little effort in the late morning period.

As with mounting attempts, the frequency of successful mounting by single males peaked in the late afternoon period (Fig. 1). The diurnal pattern in successful mounting by dominant males was similar to that of the single males. On the other hand, although the overall frequency of successful mounting by subordinate males was not different from that of the single males (Table 1), their success was significantly ($P < 0.05$) less in the late afternoon period compared to single (and dominant) males (Fig. 1).

Single males waltzed significantly more frequently in the morning period than in other periods, and the frequency remained low for the rest of the day. The pattern in dominant males did not differ significantly from that of the single males. The subordinate males, on the other hand, lacked this peak of waltzing in the morning (Fig. 1). There was no significant difference in waltzes/approach between dominant males (0.14) and single males (0.19), but the difference between single males and subordinate males (0.13) was significant ($\chi^2 = 3.94$, $P < 0.05$).

Females crouched to the approach of dominant males (0.28) and subordinate males (0.19) significantly ($P < 0.01$) less often than to single males (1.12). The ratio of crouches/approach for dominant males was 0.07 and that for subordinate males was 0.05. Both were significantly ($P < 0.005$) lower than the same ratio for single males (0.21) by χ^2 tests.

DIFFERENCES BETWEEN THE RANDOM-BRED (MM) STRAIN AND THE INBRED (I-420) STRAIN

During observations of the two-male mating groups, the frequency of interference of mating attempts of one male by another was also re-

corded. In these incidents, the competing male either (a) approached close to the mating pair, or (b) attempted to peck or dislodge the mounting male. No interference was observed in pens with two inbred males. Frequencies of interference of subordinate males' mating attempts by dominant random-bred males are shown in Table 3. The high frequency of disruption of subordinate males' mating attempts by dominant males in the late afternoon period was reflected in the low frequency of treading (Table 4), and low rate of successful copulation (Table 3) by subordinate random-bred males during that period.

While in both strains the dominant males had higher frequencies in successful mounting, treading, and tail bending than subordinate males, statistical comparisons of these two types of males with the control single males revealed interesting differences between the two strains. In the random-bred strain, the dominant males had higher frequencies of these three components of mating behavior than the single males (and the subordinate males). In the inbred strain, however, there was no significant difference between the dominant males and the single males in these components of behavior (Table 1). It was the inbred subordinate males who displayed a lower frequency of treading and tail bending compared to the inbred single males that resulted in the difference between the dominant males and the subordinate males of that strain.

TABLE 4. Temporal pattern of treading between subordinate and single males in the random-bred strain (MM = Minnesota Marker).

Male status	Frequency of treading†			
	Morning I	Morning II	Afternoon I	Afternoon II
MM single	0.2ab	0.6ab	0.8b	1.9c
MM subordinate	0.2ab	0.1a	0.2ab	0.1a

† Per male per five observations. Means followed by different letters were significantly different ($P < 0.05$).

Mating efficiency (tail bendings/mounting attempt) of random-bred dominant males (0.29) was significantly higher ($\chi^2 = 5.33$, $P < 0.05$) than that of random-bred single males (0.14). On the other hand, there was no significant difference between inbred dominant males (0.16) and inbred single males (0.09) in mating efficiency. There was also no difference in the mating efficiency between subordinate males and single males in either strain.

DISCUSSION

While some pair copulations may occur outside the female's fertilization period (e.g., Elder and Weller 1954, Fabricius and Jansson 1963, Zenone and Sims 1979), and may function as a ritual to strengthen the pair bond, almost all EPCs are directed at fertile females (Birkhead, in press), indicating that males who compete for fertilization are sensitive towards females' fertile periods. Furthermore, over and above this gross timing of the female's fertile period, timing within a diurnal cycle may be important (McKinney et al. 1984; Birkhead, in press). Artificial insemination studies in chicken and turkey showed that the fertility of eggs from the female is significantly higher with afternoon rather than morning inseminations (Moore and Byerly 1942, Malstrom 1943, Parker 1945, Christensen and Johnston 1975). Bobr et al. (1964) determined that a hard-shelled egg in the uterus at the time of insemination significantly reduced fertility. Bilgili et al. (1984) and Giesen and McDaniel (1980) showed that fertility was significantly lower if chicken hens were inseminated during the last 4 hr that the egg was in the uterus. A hard-shelled egg is more likely to be present during the morning than during the afternoon (Shimada 1980) as most hens lay their eggs in late morning and early afternoon. Furthermore, hens are less receptive to males in the morning than in the afternoon (Cheng et al. 1984). In our experiment, males alone with the females (single males) showed low frequency of mounting attempts and high frequency of waltzing in the early morning. The frequency of mounting attempts increased and the frequency of waltzing decreased in the later periods, probably related to the increasing number of hens which have laid their eggs. These results suggest that males may be sensitive to the fertile period within a diurnal cycle of the females and are maximizing their efficiency in fertilizing eggs. Wilson et al. (1979) found the testosterone

level of roosters increased throughout the day and peaked nocturnally. Lake and Wood-Gush (1956) also reported diurnal variation of semen volume in roosters, with the highest volumes obtained in the afternoon.

In domestic chickens, viable sperm can be stored in the female's sperm storage tubules for 2 weeks or more, but fertility declines with the age of sperm after the first week (Allen and Champion 1955, Payne and Kahrs 1961, Lake 1975). When hens were caught immediately after copulation and artificially inseminated with semen from a rooster of a different breed, half of the progeny were sired by each male (Warren and Gish 1943). If two inseminations were 4 hr apart, however, 80% of the progeny resulted from the second insemination (Compton et al. 1978). Semen from the two inseminations remain in separate layers in the female's sperm storage tubules, with the most recent semen being used first to fertilize eggs (Compton et al. 1978, DeMerritt 1979). Based on this mechanism, where the last sperm to enter the sperm host tubules are the first released, one would predict that in a competitive situation, males would, when possible, increase their rate of copulations to cover up semen deposited by competing males. A review of copulation behavior of birds suggests that birds breeding in colonies (with the presence of a higher number of potential sexual competitors) copulate more frequently than solitary breeding individuals of the same species (Birkhead et al. 1987). Our results with chickens support this observation. Birkhead et al. (1987) further indicated that in all situations observed so far where multiple mating by females seems likely, higher than necessary copulation rates would occur.

Time of day of matings, therefore, would also be important and males could compete by preventing subsequent copulations with the females by other males. In the company of a subordinate male, dominant males maintained a relatively high frequency of mounting attempts throughout the day, with the exception of the second morning period. Given that males have a limited amount of sperm, time, and energy, a male would increase his chances of fertilization by reducing his mating effort during this late morning period (when insemination would be least effective), and increasing his effort during other times of the day. It should also be noted that unlike single males who face no competition, dominant males have

to devote time and energy in vigilance to forestall mating attempts by subordinates. Although late afternoon would be the time when inseminations would probably be most effective, it would also be the most important time to prevent successful matings by competitors. The dominant male would have to balance his time between these two activities and this may account for our finding that dominant males showed a lower frequency of mounting attempts in the late afternoon period compared to single males. Despite a lower frequency of attempts by the dominant males, they were obtaining more successful copulations than single males (and subordinate males) during this period because of a higher rate of success. Our data (Table 3) indicated that the proportion of subordinate males' mounting attempts interfered with by dominant males was low in the late morning period when the chance of effective insemination was low. However, the frequency of interference was high in late afternoon when mating activities were high. As a result, the mating efficiency of subordinates was very low during this period when a successful insemination would likely be effective (see also Table 4). In the Guianan Cock Of The Rock (*Rupicola rupicola*), disruption of mating attempts caused females to modify their mating patterns, and males that caused intense and persistent disruption received a disproportionate share of this redirected mate choice (Trail 1985).

Subordinate males approached and attempted to mount females as often as dominant males. Despite interference by dominant males, subordinates were able to complete a number of copulations. The lower ratio of waltz/approach exhibited by subordinates, and the low frequency of females crouching to their approaches, indicated that subordinate males were spending little time in courtship but were attempting to mount the females regardless of whether they were receptive. This strategy may enable the subordinate males to increase their chance of completing more copulations in order to compete with the dominant males.

Many species which normally establish breeding territories become organized into dominance orders or despotism when forced together in small spaces (review in Wilson 1975). Evidence favoring the hypothesis of dominance advantage in reproductive competition has been persuasive (Wilson 1975). In larger flocks of chickens with larger numbers of males, revolts by subordinates

(challenging and defeating a more dominant individual) often occur and the dominance hierarchy may also not be linear. Correlation between social rank and mating frequency is only moderate (Craig et al. 1977, Kratzer and Craig 1980). In small flocks the dominance relationship is very stable. Our experiment demonstrated that if the subordinates have no other means of obtaining a genetic benefit (e.g., by emigration or by revolt), they will compete for fertilizations. Faced with competition, the dominant males increased their chances of fertilization through increased mating efficiency and copulating during the fertile periods of the females. Thus, an interplay of environmental or social perception (proximate physiological mechanisms) and hormonal responsiveness (ultimate evolutionary factors) may influence diurnal rhythms and contribute to variations in strategies of mating behavior (Crews and Moore 1986).

Kin selection might provide another means by which subordinates obtain a genetic benefit. Watts and Stokes (1971) reported that in wild turkeys (*Meleagris gallopavo*), young males form sibling groups and remain in the group for life. Only the dominant brother of the group has the privilege of mating with hens. In our inbred strain where the individuals were closely related, competition for matings was less intense than that in the random-bred strain. Although there was no difference in the mating behavior between single random-bred and single inbred males, dominant inbred males did not increase their frequency of mating activities compared to the control (single males), and no interference of mating attempts was observed. It was the subordinate inbred males who became passive in competing (since the dominant males would most likely be passing the same genes to the next generation as the subordinates themselves would?). On the other hand, although kin recognition mechanisms have been demonstrated in some quail species (Bateson 1982; Nichols and Cheng, unpubl.), none has been demonstrated in chickens. The differences between random-bred and inbred chickens observed could simply be a strain difference; they should best be viewed as observations to stimulate more research rather than evidence to support a hypothesis.

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