Applied Animal Behaviour Science, 37 (1993) 57–67

0168-1591/93/$06.00

Early exposure to the opposite sex affects mating behaviour in White Leghorn chickens

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(Accepted 12 January 1993)

Abstract

To examine the effect of early exposure to the opposite sex on mating behaviour in White Leghorns we observed interactions between males and females that had been raised with (mixed-sex) or without (same-sex) the other sex. Groups of six females and one male were assigned to one of four treatments based on how they were raised: mixed-sex females with a mixed-sex male (MM), same-sex females with a same-sex male (SS), mixed-sex females with a same-sex male (MS) and same-sex females with a mixed-sex male (SM). Observations were conducted over an 8-week period beginning when the birds were 23 weeks old. Overall, MM and SS groups had significantly more successful copulations and a higher success rate than MS and SM groups, although the increased rate was mostly because of the influence of the MM group. Female behaviour was similar among treatment groups, although more mating attempts and more successful copulations occurred with top-ranking females in the MM and SS groups. Finally, MM and SS groups initially produced more eggs than the MS and SM groups, however, this difference disappeared over time. The results of this study show that early experience with the opposite sex enhances mating success in adulthood. However, it also indicates that matching males and females for experience is of importance.

Keywords: Chicken; Mating behaviour; Sex influence

Introduction

Early social experience may have important effects on adult mating behaviour and reproductive success (e.g. Kagan and Beach, 1953; Creel and Albright, 1987; Kruijt and Meeuwissen, 1991). Studies on sexual imprinting in domestic fowl suggest that exposure to heterospecifics during critical periods in development may result in a sexual preference for those species at maturity (e.g. Schein and Hale, 1959). Likewise, social deprivation during development may result in impaired sexual behaviour during adulthood (Fisher and Hale, 1957; Vidal, 1980; see Wood-Gush, 1958 for an exception).

Exposure to the opposite sex during rearing may also influence adult sexual behaviour. Young male chickens separated from females at 58 days of age show lower levels of sexual activity than males separated at 70 days of age

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(Siegel and Siegel, 1964). However, in another study, males separated from females at 42 days of age had mating behaviour comparable with males that remained with females throughout the rearing period (Cook and Siegel, 1974). Thus the effect of exposure to the opposite sex is not yet clear.

In commercial situations, layer parent stocks can be raised from hatch to adulthood in either same-sex or mixed-sex groups. An earlier study examining the effects of these rearing conditions on male behaviour in White Leghorns indicated that males reared in mixed-sex groups were less aggressive and more sexually active than males reared in all-male groups (Leonard et al., 1993). Rearing conditions can also affect female behaviour and thus interactions between males and females. If early experience with the opposite sex enhances sexual activity in both males and females then pairs reared in mixed-sex groups should have greater mating success as adults than pairs reared separately. Pairs in which one member has had experience should have intermediate success. The purpose of our study was to examine the effects of rearing in same- and mixed-sex groups on mating behaviour and success in White Leghorn chickens.

Animals, materials and methods

Rearing conditions

At hatch, male and female White Leghorn chicks were randomly assigned to one of two all-female or all-male pens (same-sex conditions) or to one of two male-female pens (mixed-sex conditions; Table 1). Food and water were provided ad libitum during brooding and rearing. The photoperiod was gradually decreased from 23L:1D at Day 1 to 9L:15D by Week 7, after which it was constant until the end of the rearing period at 18 weeks. As part of a

Table 1
Brooding and rearing conditions for the same-sex and mixed-sex males and females

Treatment	Sex	Mean number of birds/pen	Pen size (m)
Brooding (Weeks 1–6)			
Same-sex	Male	50	3.6×5.1
Same-sex	Female	510	7.2×5.1
Mixed-sex	Male+female	46+467	7.2×5.1
Rearing (Weeks 6–18)			
Same-sex	Male	50	3.6×5.1
Same-sex	Female	445	14.4×5.1
Mixed-sex	Male+female	40+445	14.4×5.1

There were two pens for each of the combinations presented above separate study on the effect of rearing condition on productivity, the males were dubbed at hatch and both sexes were beak-trimmed at 6 weeks.

Mating behaviour observations

Housing and pen assignments

The observation area consisted of 24, 3.65×5.10-m^2 floor pens. Twelve pens lined either side of a central corridor. Each pen had a littered floor area at the front with a suspended feeder and a raised roosting area at the rear with a bell drinker and nesting box. Food and water were provided ad libitum throughout the experimental period. The photoperiod was 11L:13D at 18 weeks of age and was increased weekly by 15-min increments until it reached 14L:10D at 30 weeks.

At 18 weeks each pen of birds was transferred to an observation pen. This allowed them to become familiar with these pens before the experiment began. To examine the effect of early experience with the opposite sex on mating behaviour, we assigned six females and one male, at 22 weeks of age, to one of four treatment groups based on their rearing condition: (1) Mixed-sex females with a mixed-sex male (MM); (2) Same-sex females with a same-sex male (SS); (3) Mixed-sex females with a same-sex male (MS); (4) Same-sex females with a mixed-sex male (SM). Each of the treatment groups was replicated in six pens. The male in each group was assigned at random. The six females in each group were reared together, but had no prior exposure to the male in their treatment group. Because the birds housed at the two ends of the corridor could potentially be affected by location, blocking was used to ensure that each treatment appeared in one of the four end pens. A 0.32-cm mesh screening was placed on the front of each pen so both the observer and the birds in the pen across the corridor were less visible.

Observations

The birds in each pen were observed once a week beginning at 23 weeks of age and continuing for 8 weeks. Observations were conducted 5 days week^{-1} and were made after 08:00 and before 16:30 h. We attempted to balance observations on each pen for the time of day and the sequence through the 5-day period. Each male was observed for a total of 8 h. Fifty-seven per cent of observations were conducted before noon and 43% after noon. This was balanced across treatment groups. The observer sat in the aisle outside the pen and allowed 2 min for the birds to become accustomed to her presence. Each male was observed for 1 h and the frequency of the following behaviours were recorded continuously on a Sony Walkman WM-D6C for later transcription: (1) Successful copulation: the male mounts, treads and makes cloacal contact with the female. (2) Unsuccessful copulation: the male mounts, or mounts and treads, but cloacal contact is not made. (3) Rear approach: the male approaches a female from behind, sometimes raising his neck feathers. This was scored only if it was not followed by mounting. We considered mating attempts to be the sum of successful and unsuccessful copulations. The success rate was the number of successful copulations divided by the number of mating attempts.

We also recorded the behaviour of females during successful and unsuccessful copulations and rear approaches by the male. Female behaviour included (1) crouching: female lowers body and spreads wings (sexually receptive posture); (2) avoiding: female moves away from male; (3) ignoring: female shows no change of behaviour when approached by male; (4) crouching and running: female initially crouches, but then moves away from male as he approaches or attempts to mount; (5) escaping: male grabs female by neck, she pulls away and he releases her.

Female dominance hierarchies were determined by observing the six females in each pen during the regular observation periods and in competitive trials conducted at the end of the study. These methods gave consistent results in 93% of the trials. Before each competitive trial, feeders were removed from the pens for approximately 18 h. The feeders were then replaced, but with the access reduced to an area large enough for only two birds. Interactions among females were recorded during a daily 20-min observation period for 5 days. The order in which pens were observed was randomized for each day.

The dominance status of each female was based on the outcome of agonistic interactions between pairs of birds. An individual lost an interaction if it fled when another pecked, chased or threatened it. A female was considered dominant over another if she won more interactions than she lost with that individual. The hierarchy was determined by ranking birds according to how many individuals they dominated. To analyze the relationship between mating behaviour and female dominance, females were divided into the top, middle or lower third of the hierarchy.

The number of eggs produced per pen was recorded throughout the observation period. We corrected for mortality by using the number of eggs produced per number of females in the pen.

Analyses

We omitted Weeks 2 and 7 from the analyses because electrical problems disrupted data collection. To examine changes in behaviour over time we divided the remaining 6 weeks into three periods: early (Weeks 1 and 3), middle (Weeks 4 and 5) and late (Weeks 6 and 8).

The analyses of variance were applied in the form of a split-plot model, with the three time periods serving as sub-plots (Snedecor and Cochran, 1980). The whole-plot structure was essentially a 2×2 factorial design replicated six times. The first factor represented the comparison based on the rearing condition of the females (i.e. MM and MS vs. SS and SM) and the second factor, the comparison based on the rearing condition of the males. The interaction involved the comparison based on the rearing condition of both the male and the female. Therefore, groups where males and females were matched for rearing condition (i.e. MM and SS) were compared with groups where rearing condition differed between the two sexes (i.e. MS and SM).

We initially conducted early analyses using non-parametric methods because of some concerns that the underlying assumptions of the analysis of variance were not met. The conclusions from the two methods were identical, therefore, the analysis of variance was used throughout.

Preliminary analyses of the female dominance data indicated that the primary differences were between females ranked in the top third and middle- and low-ranking females combined. That is, the number of behavioural events (e.g. mating attempts) involving middle- and low-ranking females did not differ significantly. Here, we examine the influence of female dominance by comparing the proportion of behavioural events that involved top females for each of the four treatment groups. The percentage data were analyzed in the original scale and after applying the arcsine square-root transformation. The two analyses led to the same interpretation and hence the results are presented in the original scale. We report P values greater than 0.10 as NS.

Results

Overall, there were no significant effects of treatment on mating attempts (NS; Table 2). However, pairing effects were significant for successful copulations ($P<0.04$), with MM and SS groups having more successful copulations than MS and SM groups (Table 2). Success rate also showed a significant pairing effect ($P<0.04$). This effect was mostly due to the high success rate of the MM group (Table 2). There were no significant effects of treatment on rear approaches (NS; Table 2).

Mating attempts showed a significant pairing×time interaction ($P<0.008$; Fig. 1). In the early period the MM and SS groups tended to have more mating attempts than MS and SM groups, resulting in a near significant pairing effect ($P<0.07$; Fig. 1). However, by the late period, mating attempts showed a highly significant pairing effect with the MM and SS groups having fewer mating attempts than the MS and SM groups ($P<0.002$; Fig. 1).

Successful copulations also showed a significant pairing×time interaction ($P<0.004$; Fig. 1). The pairing effect was significant in the early period ($P<0.02$), with MM and SS groups having a higher number of successful copulations than the MS and SM groups (Fig. 1). This pattern reversed in the late period leading to a near significant pairing effect ($P<0.09$; Fig. 1). Success rate showed no significant interactions of female effects, male effects or pairing effects with time (NS in all cases).

Table 2
Mean number of mating attempts, successful copulations and rear approaches and mean success rate for each group over the three observation periods

	Treatment					
	MM	SS	MS	SM	SEM	*P*
Mating attempts	1.47	1.67	1.61	1.17	0.203	NS
Successful copulations	1.31	1.33	1.00	0.75	0.201	0.04
Success rate	0.88 (14)	0.68 (15)	0.64 (18)	0.57 (15)	0.077	0.04
Rear approaches	3.39	3.13	3.83	3.03	0.519	NS

$n=18$ for each group except for success rate where sample sizes varied, as indicated in parentheses, because there were no mating attempts in some pens during the late period. Standard errors of the means (SEM) are based on $n=15$ for success rate and $n=18$ for the other variables. Estimates of SEM are based on 15 d.f.

Rear approaches showed a significant male×time interaction ($P<0.001$; Fig. 1). In the early period the mixed-sex males (i.e. males in treatment groups MM and SM) performed significantly more rear approaches than the same-sex males (i.e. males in treatment groups SS and MS; $P<0.05$; Fig. 1). Conversely, in the late period the mixed-sex males performed significantly fewer rear approaches than the same-sex males ($P<0.01$; Fig. 1).

Female behaviour and mating

Females crouched during 98% of all successful copulations and 81% of all unsuccessful copulations. They also crouched and ran during an additional 14% of unsuccessful copulations and escaped after being grabbed by the male during the remaining 5% of unsuccessful copulations. There were no significant effects of treatment on the proportion of each response during unsuccessful copulations (NS in all cases).

Females avoided males during 60% of all rear approaches. They crouched during 15%, ignored the male during 14%, crouched and then ran during 9.5%, and escaped during 1.5% of all rear approaches. Again, no effects were significant. However, mixed-sex males tended to be ignored by females proportionally more often than same-sex males (38.3% and 20.8%, respectively; $P<0.07$) and mixed-sex females ignored males proportionally more often than same-sex females (38.4% and 20.7%, respectively; $P<0.06$).

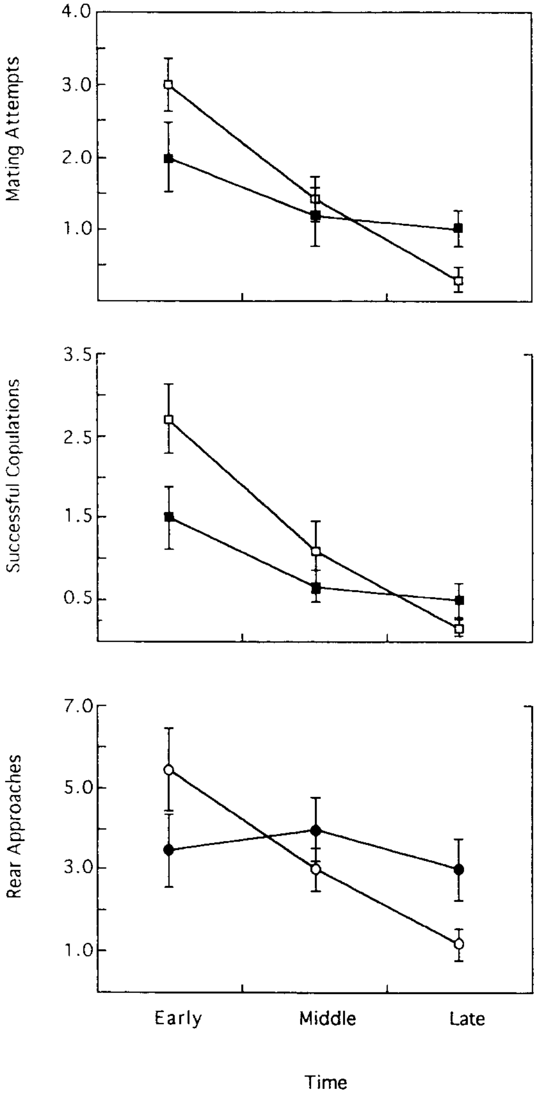

Fig. 1. Mean (±SEM) number of mating attempts, successful copulations and rear approaches during the early, middle, and late time periods. Mating attempts and successful copulations compare MM and SS groups (□) with MS and SM groups (■). Rear approaches compare MM and SM groups (○) with MS and SS groups (●).

Female dominance and mating

When analyses were carried out on the top-ranked females both mating attempts and successful copulations showed a significant pairing effect ($P < 0.03$). That is, proportionally more mating attempts and more success-

Table 3
Proportion of mating attempts, successful copulations and rear approaches with top-ranked females for each group over the observation period

	Treatment					
	MM	SS	MS	SM	SEM	*P*
Mating attempts	0.38	0.37	0.18	0.12	0.089	0.02
Successful copulations	0.38	0.44	0.17	0.08	0.115	0.03
Rear approaches	0.24	0.19	0.35	0.25	0.050	NS

Number of pens where we determined hierarchies: MM: $n=6$; SS and MS: $n=5$; SM: $n=4$. The standard errors of the means (SEM) are based on sample size $n=5$.

ful copulations were directed to top-ranking females in the MM and SS groups than in the MS and SM groups (Table 3). There was no significant effect of treatment on rear approaches (NS; Table 3).

Egg production

Egg production showed no significant treatment effects nor interactions of treatment with time (NS in all cases). However, when egg production was analyzed on a week by week basis, there was a significant pairing effect in the first week ($P<0.02$), with MM (0.76) and SS (0.78) groups producing more eggs/hen/day than the MS (0.71) and SM (0.64) groups.

Discussion

The results of this study indicate that early exposure to the opposite sex influences adult mating behaviour. As predicted, groups in which both males and females had experience with the opposite sex (i.e. MM groups) had the highest overall success rate. However, rather surprisingly, inexperienced groups (i.e. SS) had as many successful copulations overall as experienced groups and a success rate higher than the treatments in which males and females differed in their experience (i.e. SM and MS). In addition, both experienced and inexperienced groups produced more eggs initially than the groups with mixed experience.

In this study mating efficiency (success/attempt) was highest in the experienced group. Research on the effects of breeding experience/age on reproductive success indicates that experienced pairs are often more successful at producing and rearing offspring than inexperienced pairs (e.g. Coulson and Thomas, 1983; Rowley, 1983). Although the birds in our study were the same age, the mixed-sex group had the opportunity to engage in some sexual activity before full maturity. Our results suggest that this early experience may be advantageous, provided both males and females have the same experience.

Success may be based not only on the experience of each partner, but also on the compatibility of the pair (Coulson, 1972; Rowley, 1983). For instance, in the Kittiwake Gull (*Rissa tridactyla*) breeding failure has been attributed to the compatibility of the pair in establishing incubation schedules (Coulson, 1972). In our study the inexperienced group had as many successful copulations overall as the experienced group and more than the groups with mixed experience. Thus pairs with similar early experience may develop the same, or at least compatible, copulatory behaviours.

It is not clear, however, what factors influence compatibility between partners in domestic fowl. Rushen (1983) found that mating attempts in a Rhode Island Red×White Leghorn cross were unsuccessful when the male approached without specific courtship behaviours or when the female did not crouch. In our study, females crouched during 81% of all unsuccessful copulations and, in general, female responses to male approaches were independent of the experience of either sex. However, detailed observations of both sexes may reveal more subtle differences in male–female interactions associated with the similarity of their early experience.

In general, all groups showed a decline in mating attempts and successful copulations over time. However, the effect was more dramatic for the groups matched for experience. The MM and SS groups had more mating attempts and successful copulations in the early observation period than the SM and MS groups but, by the end, they had significantly fewer attempts and similar numbers of successful copulations. A decline in sexual activity with time has been reported for domestic fowl (Duncan et al., 1990). These authors showed that initial levels of activity in broiler breeders are higher than what is necessary to maintain fertility. They suggested that sexual behaviour may also serve a non-reproductive function, such as improving group cohesiveness or strengthening the pair-bond. Groups matched for experience may have had a relatively more dramatic decline in activity because their initially higher levels of sexual activity resulted in social bonds forming earlier than in groups with mixed experience.

The social status of the female did not seem to influence mating attempts and successful copulations in the groups matched for experience. In both groups, mating attempts and copulations with top-ranking females appeared to be in proportion to their numbers. These results are consistent with those of Rushen (1983), who found no relationship between sexual activity and female status. However, this was not the case for the groups with mixed experience. Proportionally fewer of their mating attempts and successful copulations were with top-ranking females. These results are consistent with earlier work (e.g. Guhl et al., 1945) which found a negative correlation between female rank and mating success. Thus the relationship between rank and success is not consistent among treatment groups. Again it is not clear why the effect of female rank would differ between groups matched and unmatched for experience.

Little is known of the effect of mixed- vs. same-sex rearing on mating behaviour in chickens. Earlier work by Siegel and Siegel (1964) suggested that limiting exposure to females during development resulted in decreased sexual activity of males at maturity. In contrast, Cook and Siegel (1974) observed that early exposure to females had little effect on the subsequent mating behaviour of males. It was not clear from either study how the females were reared. Differences in female rearing conditions might explain these and other apparently contradictory results.

In conclusion, this study shows that exposure to the opposite sex during development influences mating behaviour and that the most effective method for raising parent layer stocks may be to rear males and females in mixed-sex groups from hatch. When this is not possible, a reasonable alternative would be to ensure that both males and females are reared with the same exposure to the opposite sex.

Acknowledgements

We thank Gail Butler, David Fraser, Andy Horn and two anonymous reviewers for reading the manuscript and providing many helpful comments. We also thank Michael Clinchy for his help with the data collection. This study was supported in part by financial aid from Shaver Poultry Breeding Farms Limited. Centre for Food and Animal Research Contribution No. 2069. Research Program Service Contribution No. R123.

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