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Early exposure to females affects interactions between male White Leghorn chickens

Marty L. Leonard, Liana Zanette and R. Wayne Fairfull
Centre for Food and Animal Research, Agriculture Canada, Ottawa, Ont. K1A 0C6 Canada

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ABSTRACT

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To examine the effect of rearing condition on White Leghorn chickens we observed interactions between pairs comprising one male reared in an all-male group (single-sex) and one male reared with females (mixed-sex). Two males, one from each treatment, were placed in a neutral arena with either a stuffed female chicken (model) or a white jug which served as a control stimulus (control). Trials were conducted both before (20 weeks of age) and after (47 weeks of age) single-sex males were exposed to females. At 20 weeks, mixed-sex males displayed significantly more sexual behaviour in the presence of a female model than did single-sex males. In contrast, single-sex males were significantly more aggressive than mixed-sex males during the control presentation. At 47 weeks mixed-sex and single-sex males did not differ in the frequency of either sexual or aggressive behaviours. This result was due to a decrease in the frequency of sexual behaviours by mixed-sex males and of aggressive behaviours by single-sex males. Our results suggest that rearing males in all-male groups may decrease sexual behaviour and increase aggressive behaviour, but that the difference disappears with age and/or adult exposure to females.

Keywords: Chicken; Sexual behaviour; Agonistic behaviour

INTRODUCTION

The effect of early social experiences (e.g. rearing condition) on adult sexual behaviour in domestic fowl has been well studied (e.g. Wood-Gush, 1958; Siegel and Siegel, 1964; Kruijt, 1971; Cook and Siegel, 1974). Chickens reared in isolation show impaired sexual behaviour as adults (Vidal, 1980). Likewise, rearing in single-sex groups may also influence adult sexual behaviour. Males separated from females at 54 days of age show lower levels of sexual activity than males separated at 70 days (Siegel and Siegel, 1964).

Early social experiences may also affect intrasexual behaviour (Creel and Albright, 1987). Rearing condition appears to influence the agonistic behav-

Correspondence to: M.L. Leonard, Centre for Food and Animal Research, Agriculture Canada, Ottawa, Ont. K1A 0C6, Canada.

iour of young female chickens (Lee and Craig, 1980). However, little is known of the influence of early experience on interactions between males.

In some commercial situations layer parent stocks are raised from hatch to adulthood in single-sex groups. The effect of this practise on the sexual and agonistic behaviour of sexually mature males is unknown. The purpose of our study was to examine the effect of early experience on interactions between White Leghorn males. Specifically, we examined the effect of brooding and rearing in single- versus mixed-sex groups. We also tested whether these effects were modified by adult experience. Because we cannot separate the effect of age from that of adult experience (i.e. exposure to females), we refer to the two processes as 'adult experience'.

METHODS

General rearing conditions

At hatch, male (Strain B) and female (Strain C) White Leghorn chicks were randomly assigned to one of two rearing conditions: (1) single-sex: the sexes were brooded (Weeks 1–6) and reared (Weeks 6–18) in different pens; (2) mixed-sex: the sexes were brooded and reared together. Individuals in the single-sex group were randomly assigned to one of two all-female or all-male pens, while individuals in the mixed-sex group were randomly assigned to one of two male-female pens (Table 1). During brooding and rearing the

TABLE 1

Pen assignments during brooding, rearing and adult housing for single-sex and mixed-sex males. At adult housing the single-sex males and females were mixed. There were two pens for each of the combinations presented below. Excess birds, used as replacements for mortalities, were randomly removed at the end of brooding at 6 weeks, and at the end of rearing

Treatment	Sex	Mean number of birds per pen	Pen size (m)
Brooding (Weeks 1–6)			
Single-sex	Male	50	3.6×5.1
Single-sex	Female	510	7.2×5.1
Mixed-sex	Male+Female	46+467	7.2×5.1
Rearing (Weeks 6–18)			
Single-sex	Male	50	3.6×5.1
Single-sex	Female	445	14.4×5.1
Mixed-sex	Male+Female	40+445	14.4×5.1
Adult (Weeks 18+)			
Single-sex	Male+Female	37+406	14.4×5.1
Mixed-sex	Male+Female	37+406	14.4×5.1

chicks were fed ad libitum. 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 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.

At 18 weeks (adult housing) individuals from the two pens of single-sex males (with the exception of 26 males kept in all-male groups for Experiment 1) were randomly placed into the two female pens (Table 1). To control for the effect of familiarity between the sexes we also exchanged males from the mixed-sex pens. Males were wing-tagged with large, individually numbered tags. Adults were fed ad libitum. The photoperiod was gradually increased from 10L:14D at 18 weeks to 14L:10D by 34 weeks after which it was constant until the end of the observation period.

Experiment 1: the effect of early experience

At 20 weeks of age, 26 mixed-sex males were randomly selected for the male competition experiment. The 26 single-sex males used in this experiment had been randomly selected at 18 weeks and had no prior exposure to females. Pairs comprising one single-sex and one mixed-sex male were placed for 20 min on a 3 m$\times$6 m cement floor covered with wood shavings (arena), with either a taxidermic mount of a sexually mature female in a standing posture (model trials) or with a 24 cm high white jug with a red cap (control trials). Each male was tested only once. Twenty-four hours before each trial, nine single-sex and nine mixed-sex males were removed from their home pen and placed in identical, but separate, holding pens.

Trials were conducted between 08:30 and 16:00 h over 4 days. Seventeen model trials and nine control trials were balanced for time and day. We alternated presentations of two identical female mounts during the model presentations. At the beginning of each trial both males were removed from their holding pens and simultaneously placed in the arena.

An observer, blind to the rearing condition of each male, sat behind an opening in a large partition on one side of the arena. The frequency of the following behaviours were recorded verbally using a Sony Pro Walkman for later transcription.

(1) Waltzes to the stimulus. The male drops his wing and circles the stimulus with short steps. We consider the waltz to be directed to the stimulus if it was performed <0.5 m from the model while the other male was >0.5 m.

(2) Neck grasps. The male grasps the feathers at the back of the neck of either the model or the other male.

(3) Attempted mounts. The male places one of his legs on either the stimulus or the other male.

(4) Mounts. The male stands on either the stimulus or the other male and may or may not tread.

(5) Waltzes to the male. We considered the waltz to be directed to the other male if both males were > 0.5 m from the stimulus.

(6) Frontal attacks. The male lunges at the stimulus or the other male and strikes with beak or spurs.

(7) Hard pecks. The male pecks the stimulus or the other male with force.

(8) Chases.

(9) Crows.

We considered behaviours to be distinct if they were separated from another behaviour by 5 s. We pooled neck grasps, attempted mounts and mounts into a single class referred to as 'sexual behaviour'. We also pooled frontal attacks, hard pecks and chases into a single class referred to as 'aggressive behaviour'. Waltzes can be performed in both sexual and aggressive contexts (Wood-Gush, 1956). We included 'waltzes to the stimulus' in the 'sexual behaviour' category if the waltz was preceded or followed by another sexual behaviour or if no aggressive behaviour was directed toward the stimulus. We included 'waltzes to the male' in the 'aggressive behaviour' category if the waltz was preceded or followed by another aggressive behaviour or if no sexual behaviour was directed to the male.

In addition, we recorded the proportion of time each male spent < 0.5 m from the stimulus (close) and > 1 m from the stimulus (far). The time taken by the male to reach < 0.5 m from the stimulus and the time to interact with the stimulus were also recorded.

We determined the dominant male of each pair based on the outcome of all aggressive interactions. An individual lost an aggressive interaction if it fled from or avoided the other male (who was considered the winner). A tie occurred if both birds stood their ground. An individual was considered dominant if it won all interactions during a trial and subordinate if it lost all interactions. In cases where reversals occurred (i.e. individuals won and lost interactions in the same trial in two of 19 cases) then it was considered dominant if it won more interactions than it lost and if it won the last two consecutive interactions of the trial.

Experiment 2: the effect of adult experience

At 47 weeks we repeated the above experiment using 36 males that had been initially brooded and reared with the sexes separate and 36 males that had been brooded and reared with the sexes mixed. In this experiment the single-sex males had now been exposed to females for 29 weeks. Experimental protocol was as described above except that we completed 22 model trials and 14 control trials.

Morphometrics

Body-weight (kg), tarsus length (cm), comb length (cm), wattle length (cm), and wattle width (cm) at the widest point were measured for each male at 18 weeks and at 47 weeks of age. Comb length is highly correlated with comb height and area in some strains of White Leghorn (Graves et al., 1985). Because our males were dubbed we used comb length as a measure of comb size.

Analyses

With the exception of the morphometric measurements, non-parametric statistics were used throughout. We present means ± standard errors (SE). We report P values greater than 0.10 as NS. Male response was not dependent on which of the female models was used. Therefore, the data from the two models were pooled. We also pooled the data for mornings and afternoons because presentations were balanced for time of day.

RESULTS

Experiment 1: the effect of early experience

Sexual behaviour

Sexual behaviours were observed only during the model trials and were directed only toward the model. Males waltzed to the model, neck grasped, attempted to mount, mounted and treaded the model. Males also spent time close (< 0.5 m) to the stimulus during the model trials only.

During the model trials, mixed-sex males displayed significantly more sexual behaviour than single-sex males and they also spent proportionally more time close (< 0.5 m) to the model (Table 2). Mixed-sex males took significantly less time to reach < 0.5 m from the model and to interact with the model (Table 2).

TABLE 2

Mean (± SE) responses to the female model for 17 pairs of males (one single-sex and one mixed-sex) at 20 weeks of age. Males were compared using a Wilcoxon paired-sample test except for 'Time to interact' which was compared using a Mann-Whitney U-test because sample sizes were not equal (i.e. single-sex males did not always interact with the model)

Behaviour	Single-sex	Mixed-sex	P
Sexual behaviours	0.12 ± 0.08	16.4 ± 6.90	0.001
Proportion time < 0.5 m	0.22 ± 0.04	0.50 ± 0.07	0.01
Time to reach < 0.5 m (min)	3.44 ± 0.81	0.85 ± 0.41	0.03
Time to interact (min)	7.63 ± 1.79	2.78 ± 1.99	0.05

TABLE 3

Mean (± SE) responses for single-sex and mixed-sex males during the control ($n=9$) and the model ($n=17$) trials at 20 weeks of age. Single-sex and mixed-sex males were compared using a Wilcoxon paired-sample test

Behaviour	Control			Female model		
	Single-sex	Mixed-sex	P	Single-sex	Mixed-sex	P
Aggressive behaviours	16.70 ± 4.57	2.55 ± 1.85	0.04	5.29 ± 2.01	3.24 ± 1.63	NS
Crows	2.33 ± 1.56	3.89 ± 2.86	NS	8.11 ± 2.17	3.65 ± 1.35	0.05
Proportion time > 1 m	0.77 ± 0.06	0.87 ± 0.05	0.01	0.38 ± 0.06	0.20 ± 0.05	0.05

Aggressive behaviour

Single-sex males were significantly more aggressive than mixed-sex males during the control trials, but not during the model trials (Table 3). Single-sex males also crowed significantly more often during the model trials (Table 3). Finally, single-sex males spent significantly less time far (> 1 m) from the stimulus in the control trials and significantly more time far from the stimulus in the model trials (Table 3).

The single-sex male was dominant to the mixed-sex male in seven of nine control trials (Fisher's $P=0.06$). Because there were relatively fewer aggressive interactions during the model trials we were able to determine dominance status in only ten of the 17 pairs and single-sex and mixed-sex males were dominant equally often (five of ten trials).

The presence of the female model appeared to have some influence on the dominance status of mixed-sex males. That is, if a mixed-sex male interacted with the model before interacting with the other male, then the mixed-sex male was dominant in subsequent interactions (four of five cases). If however, the mixed-sex male interacted with the single-sex male first it was subordinate in the following interactions (four of four cases; $P=0.08$).

Experiment 2: the effect of adult experience

Sexual behaviours

As in Experiment 1, sexual behaviour was observed only during the model presentations and directed to the model only. Again, males waltzed to the model, neck grasped, attempted to mount, mounted and treaded the model. Males also spent proportionally more time close (< 0.5 m) to the stimulus during the model presentations (control: 0.002 ± 0.001, model: 0.25 ± 0.33, Mann-Whitney U-test, $Z= -5.01$, $P<0.001$).

However, unlike Experiment 1, single-sex and mixed-sex males responded similarly to the female model. That is, differences in the frequency of sexual behaviours, proportion of time spent close (<0.5 m) to the model, time to reach <0.5 m from the model and time to interact with the model did not differ significantly (NS in all cases).

Aggressive behaviours

In contrast to Experiment 1, single-sex and mixed-sex males were equally aggressive and spent a similar proportion of time far (>1 m) from the stimulus in both the control and the model presentations (NS in all cases). However, as in Experiment 1, single-sex males crowed significantly more often during the model presentations (single-sex: 17.59 ± 2.79, mixed-sex: 9.14 ± 1.95; $Z=-2.03$, $P=0.04$).

In this experiment males either did not interact aggressively (control: $n=6$; model: $n=9$) or they won interactions an equal number of times (ties = three in both cases). Therefore, we could determine which male was dominant in only five of 14 control trials and ten of 22 model trials. Single-sex males were dominant to mixed-sex males during four of five control trials (NS) and six of ten model trials (NS).

The similarity in response of single-sex and mixed-sex males to the female model during Experiment 2 appeared to be due to a decrease in the response of the mixed-sex males. That is, mixed-sex males performed significantly fewer sexual behaviours in Experiment 2 than in Experiment 1 (Experiment 2: 4.14 ± 1.71; $Z=-1.99$, $P=0.05$; see Table 2 for Experiment 1). Mixed-sex males also spent significantly less time close to the model in Experiment 2 (Experiment 2: 0.24 ± 0.06; $Z=-2.76$, $P=0.01$). However, although both increased, the time taken to reach <0.5 m from the model and the time taken to interact with the model were not significantly different between Experiments 1 and 2 (Experiment 2: 2.40 ± 0.99; $Z=-0.52$, NS and 5.56 ± 1.85; $U=23.5$, NS, respectively).

The similarity in aggression level between the males during Experiment 2 appeared to be due to a change in the response of single-sex males. That is, single-sex males performed significantly fewer aggressive behaviours during the control presentations in Experiment 2 as compared with Experiment 1 (Experiment 2: 1.43 ± 0.62; $Z=-3.49$, $P<0.001$) and they also increased the proportion of time spent >1 m from the stimulus during this time (Experiment 2: 0.93 ± 0.02; $Z=-2.27$, $P=0.02$).

Morphometrics

With the exception of tarsus length, there was a significant increase in all body measurements between 18 and 47 weeks of age ($P<0.001$ in all cases). At 18 weeks, single-sex males had significantly longer combs (single-sex: 5.4 ± 0.1, mixed-sex: 5.0 ± 0.1; Paired t-test, $t=-2.28$, $P=0.027$) and wider wattles (single-sex: 3.7 ± 0.1, mixed-sex: 3.5 ± 0.1; $t=-2.28$, $P=0.027$) than mixed-sex males. However, by 47 weeks differences in morphology between single-sex and mixed-sex males were not significant.

DISCUSSION

The effect of early experience

The results of this study suggest that rearing condition affects the behaviour of adult males. At 20 weeks of age males that had been reared with females showed more sexual behaviour toward the female model than did males reared without female contact. In contrast, single-sex males were significantly more aggressive than mixed-sex males when the model was not present.

Our results suggest that rearing in all-male groups had either (1) a direct effect on the sexual response of single-sex males or (2) caused increased aggressiveness which then interfered with sexual activity. Exposure to females before maturity may increase sexual activity in young male chickens (Guhl and Warren, 1946; Siegel and Siegel, 1964), which suggests that exposure to females may directly affect sexual behaviour. Alternatively, a negative correlation between the frequency of aggressive and sexual behaviours has been reported for inexperienced cocks (Wood-Gush, 1958) and turkey poults (Schein and Hale, 1959) suggesting that increased aggression may be associated with a decrease in sexual behaviour. We are unable to distinguish between these possibilities.

With the exception of comb size, single-sex males were not larger than mixed-sex males, suggesting that the tendency of single-sex males to be dominant was not simply related to body size. Comb size, however, may be a relatively reliable predictor of dominance relations in domestic chickens (Allee et al., 1939; Collias, 1943). Comb size is highly correlated with testosterone levels in both domestic and jungle fowl (*Gallus gallus*; Allee et al., 1939. Collias, 1943; Marks et al., 1960; Graves et al., 1985; Ligon et al., 1990) and testosterone has a direct effect on aggressive behaviour (Allee et al., 1939; Harding, 1983).

Interestingly, the presence of the female also appeared to influence the outcome of agonistic interactions. Although mixed-sex males were generally subordinate during the control trials, they were dominant as often as single-sex males in the presence of the female model. The status of the mixed-sex male seemed to be enhanced if it interacted with the female model before interacting with the other male.

Effects of adult experience

The disappearance of behavioural differences between the single- and mixed-sex males after a further 29 weeks of mixed-sex housing could be due to either the effect of exposure to females or to maturation with increased age. The change in behaviour was the result of a reduction in the frequency of sexual behaviours by mixed-sex males and in aggressive behaviours by single-sex males. A general decline in sexual activity with age has been reported for domestic fowl (e.g. Duncan et al., 1990; Ottinger, 1991). Young males appear to copulate more often than is necessary to maintain high levels of fertility (Duncan et al., 1990) suggesting that early sexual behaviour may serve a social function (e.g. building a bond between the male and female). Thus the patterns of sexual activity observed in this study may be explained in a similar way.

CONCLUSIONS

The results of this study suggest that rearing in all-male groups affected the behavior of males during male–male interactions. Individuals reared in all-male groups were initially more aggressive than individuals reared with females, while males reared with females were initially more sexually active. These differences disappeared after extended exposure to females. The results of this study indicate that rearing males in mixed-sex groups may have advantages over rearing the sexes separately.

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