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Effect of male-to-male aggressiveness and feed-restriction during rearing on sexual behaviour and aggressiveness towards females by male domestic fowl

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Abstract

This experiment was one part of a larger study investigating problems of aggression towards females by male broiler breeder fowl. To investigate causal mechanisms, we were interested in determining (1) if feed-restriction during rearing affects behaviour towards females at sexual maturity and (2) if aggressiveness towards females is correlated with general levels of aggressiveness. We compared broiler breeder males with commercial laying strain males, which were either fed ad libitum or were feed-restricted during the rearing phase, and with game strain males, bred for fighting. Differences in behaviour were determined by observing males during interactions with small groups of females.

Laying strain males did not behave aggressively towards females, whether feed-restricted or fed ad libitum during rearing. Despite genetic selection for fighting ability, game strain males also were not aggressive towards females. Conversely, broiler breeder males displayed significantly higher levels of aggression towards females than did feed-restricted laying strain males ($P < 0.02$). Broiler breeder males were rough with females during mating, whereas laying strain and game strain males were not. Females struggled more frequently during mating attempts by broiler breeder males ($P < 0.002$) and interfered frequently when these males attempted to mate with other females.

From our results, we conclude that (1) feed-restriction during rearing has little effect on the sexual and aggressive behaviour of laying strain males at maturity and (2) selection for aggressiveness has not resulted in males which are more aggressive to females. Aggression towards females appears to be a unique problem occurring in broiler breeder male strains and not a function of feed-restriction. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

This experiment was conducted as part of a larger study investigating problems of aggression towards females by male broiler breeder fowl. The poultry industry has expressed concern about increasing aggressiveness of broiler breeder males, resulting in reduced fertility, increased female injury and increased female mortality (Ouckama, personal communication; Mench, 1993). Severe injuries to females include lacerations along the torso and to the back of the head, raising concerns of reduced animal well-being. Aggression towards females by mature male fowl is unusual (Wood-Gush, 1956, 1958a; Kruijt, 1964; Craig and Bhagwat, 1974; Ylander and Craig, 1980; Rushen, 1983/1984; Bshary and Lamprecht, 1994), since males and females have separate social hierarchies with males dominating females passively (Guhl, 1949). Aggressiveness of broiler breeder males towards females may have arisen due to the management practice of feed-restriction or due to genetic effects. In a series of experiments, we examined the effects of feed-restriction and genetic strain on the behaviour of male domestic fowl. In the current experiment, the behaviour of males towards females was examined.

Broiler breeder fowl are severely feed-restricted to avoid physical and reproductive problems associated with obesity (North and Bell, 1990). Broiler breeders feed-restricted according to management guidelines show strong motivation to eat, both before and after consumption of the daily ration (Savory et al., 1993). High levels of stereotypic spot-pecking and increased activity levels relative to ad libitum fed birds suggest that broiler breeders experience frustration and suffering as a result of feed-restriction (Kostal et al., 1992; Savory and Maros, 1993; Hocking et al., 1996). Frustration associated with feeding has been shown to increase aggression of laying strain males towards females (Duncan and Wood-Gush, 1971). Our previous research indicated that feed-restriction of males during the breeding phase did not increase aggressiveness towards males or towards females. However, treatments were only imposed at sexual maturity; broiler breeder males were feed-restricted during rearing and laying strain males were not (Millman et al., 1996, 1997). During the rearing phase, feed-restricted broiler breeders display more aggression at the feeder than do broiler breeders fed ad libitum and with skip-a-day feeding, this aggression is most pronounced on off-feed mornings when feed is expected, (Mench, 1988; Shea et al., 1990). Experience during rearing can affect social behaviour of chickens at maturity (Fisher and Hale, 1957; Wood-Gush, 1958a, 1960; Leonard et al., 1993a, b). Chicks of both domestic fowl (Andrew, 1966) and jungle fowl (Kruijt, 1964) display elements of aggressive and copulatory behaviour that further develop during the first months of age. Feed-restriction of broiler breeder fowl is severe during this early stage of development and could affect ontogeny of social behaviour. We were interested in the effects of feed-restriction during rearing on social behaviour of males at maturity. Our hypothesis was that males feed-restricted during rearing would display more aggression towards females than would males fed ad libitum.

It is also possible that broiler breeder males are extremely aggressive towards females as a result of genetic selection, either inadvertently during line breeding for meat production traits, or intentionally in an attempt to improve sexual vigour. Previously, we found that broiler breeder males displayed much more aggression towards females than did laying strain males (Millman et al., 1997). Broiler breeder males aggressively pecked females,

chased them and forced copulations, whereas such behaviour was rare in laying strain males. Broiler breeder males also displayed more aggression towards other males than did laying strain males, when males were housed in pairs with small groups of females. As androgens facilitate both aggressive and copulatory motivation in avian species (Harding, 1983, 1986), one would expect aggression and mating to be correlated. Kruijt (1964) found aggressive and copulatory behaviour to be integrated in social ontogeny and it has been suggested that courtship displays reflect conflicting sexual, aggressive and escape motivation in the male domestic fowl (Wood-Gush, 1954, 1956). Therefore, it is curious that selection for high mating frequency does not appear to affect male-to-male aggressiveness (Siegel, 1959; Wood-Gush, 1960; Siegel, 1972). While Wood-Gush (1958b) found no significant difference between high and low mating lines in a male-to-male aggression test, there was some evidence that males of the low mating line were more aggressive to females. Centuries of selection for fighting ability in game-cocks has resulted in extremely high aggressive motivation and differences between strains for fighting elements (Atkinson, 1977). We were curious to see if selection for aggressive motivation has resulted in increased aggression towards females. Our hypothesis was that broiler breeder and game strain males would be similar in displaying much more aggression towards females than laying strain males. We also expected game strain males to perform forced copulations that we had previously observed in broiler breeder males.

2. Materials and methods

Procedures carried out in this study were approved by the University of Guelph Animal Care Committee, according to the guidelines of the Canadian Council for Animal Care.

2.1. Treatments

Treatments were arranged in an incomplete factorial design. Genetic effects on the behaviour of male domestic fowl towards females were determined using strains of male selected for meat production, egg production and cock-fighting. Males of a broiler breeder (BR) strain (Ross) were compared with commercial laying strain males (ISA Brown) and with a 'pit-game' line of Old English Game (GA) strain males (Pine Albany) during interactions with females of a broiler breeder strain (Arbor Acres). The effects of feed-restriction during the rearing phase were also examined using two feeding regimens. Laying strain males were randomly assigned to be feed-restricted (LR) or fed ad libitum (LA) during the rearing and breeding phases. Broiler breeder males were feed-restricted, and game strain males were fed ad libitum, during the rearing and breeding phases.

2.2. Birds

With the exception of game strain males, all birds were obtained from local hatcheries as day-old chicks and were vaccinated against the standard local diseases. Chicks did not have their combs dubbed and were not toe-trimmed. Chicks were housed at the Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA) Arkeell Poultry Research Station as

groups of 30 individuals in 3.4 m × 3.7 m pens, with pine shavings as litter. There were eight pens of females, and one pen of each of the male treatments. Males and females were reared in separate rooms with no visual, but some auditory communication possible between rooms. At 1 week of age, all chicks were beak-trimmed to prevent feather pecking and were wing-banded for identification. Following the first few days of continuous light, lighting was provided, at 10 lx, on a 8L:16D schedule during the rearing phase. Broiler breeder males and females were feed-restricted according to the management guidelines for each strain (Arbor Acres Farms, 1995; Ross Breeders, 1997). Laying strain males in the LA treatment were provided with food ad libitum. Feed-restriction of LR males was determined by maintaining a LR:LA body weight ratio equivalent to that of feed-restricted and full-fed broiler breeder males of a similar age (North and Bell, 1990). All birds were fed a mash grower diet (Leeson and Summers, 1991), with all males and a sample of females weighed weekly.

At 21 weeks, day length was gradually increased to 16 h, with lights on at 05.00 h and off at 21.00 h. Females were fed a laying ration (Leeson and Summers, 1991) and were provided with nestboxes. Nine males were selected from each treatment and placed in individual pens. Individual males were selected from the middle range of body weight for each treatment, based on good conformation of feet and legs. Laying strain males were housed in 1.8 m × 1.2 m (2.16 m²) pens. Broiler breeder males were placed in 1.5 m × 1.5 m (2.25 m²) pens in a separate room in the same building. All males had visual access to neighbouring males and had pine shavings as litter.

Game strain males were obtained on loan from a local breeder. Although cock-fighting is illegal in Canada, it is still legal in some states in the USA. The males loaned to us were one generation removed from 'pit' or fighting stock. Males were brooded by an Old English Game female and reared out of doors in a flock of mixed age and sex. Prior to sexual maturity, males were individually penned with visual access, but no physical access, to other males. The males were approximately 28 weeks of age when we obtained them. They did not have their combs dubbed, and were not beak-trimmed or toe-trimmed. The males were mature, but sexually inexperienced. However, the males had received social experience with mature and immature females during the rearing phase.

Game strain males were housed at the OMAFRA Isolation Unit to avoid disease transmission from these males to the Arkell research flocks. Males were individually housed in 1.2 m × 1.2 m pens with pine shavings as litter and a perch located 0.6 m above the floor. The pens had solid sides and PVC piping was installed at the edges of the pen doors to prevent fighting between neighbouring males. At the request of the breeder, game strain males were fed ad libitum a mixture of standard chicken grower mash (Leeson and Summers, 1991), pigeon seed, scratch grains and fresh fruit. The game males were initially very 'flighty', but frequent handling reduced their fearfulness before observations began. Although most males did not display aggression to human handlers, particular individuals were extremely aggressive and had to be handled with care.

Nine game strain females were also obtained on loan from the local breeder. Three females were of the Asil strain and six were of the Pine Albany strain. Game females were housed in groups of three in 1.8 m × 1.2 m pens, with pine shavings as litter, nestboxes and a perch provided 0.6 m above the floor. Game females were fed ad libitum, the same diet provided to game males, but with the inclusion of oyster shell. Game females were

extremely 'flighty', despite efforts to habituate them to human handlers. Feather pecking was a persistent problem in one pen, requiring separation of one female to allow her feathers to re-grow before testing with males began.

Fifty broiler breeder females were moved from the Arkell facility to the Isolation Unit for testing with game strain males. Females were group-housed in a room measuring 7.25 m² and were provided with nestboxes on the floor and pine shavings as litter. Feeding and lighting programs were maintained according to the management guidelines (Arbor Acres Farms, 1995).

2.3. Experiment 1

2.3.1. Testing

Tests were performed in a separate room of the building in which the birds were housed and began when the birds were approximately 31 weeks of age. There were three test pens in the room, measuring 1.2 m × 2.4 m with solid sides, pine shavings for litter, a nestbox and a perch 0.6 m above the ground. Mesh netting covered the top of each pen to prevent escape and along the front of the pen to act as a door. A video camera was placed on a tripod approximately 1 m in front of each pen to record the behaviour of the birds.

Males of the same treatment were tested at the same time, due to game strain males being housed in a different location from the other treatments. The testing procedure involved carrying the male in an upright position to the test pen. Three males were tested simultaneously and each male was always tested in the same pen with the same individual males as neighbours. When all three males were placed in the test pens, three broiler breeder females were placed in each of the pens. Females were randomly assigned to males and were carried individually in an upright position to the test pen. Males were always tested with the same three females and no female was assigned to more than one male throughout the experiment.

Testing began three hours prior to lights-out and behaviour was video-recorded following mixing for 2 h, from 18.00 to 20.00 h. The birds were fed in the test pen the following morning and behaviour was video-recorded for 2 h during the second evening, when the birds had been housed together for 26 h. Tests for the nine males in each treatment were completed within 1 week (Trial 1). Tests were repeated after 4 weeks (Trial 2). Immediately prior to testing, all males were subjected to a male-to-male aggression test (Millman and Duncan, 2000), during which responses towards a frozen male model were measured.

2.4. Behavioural observations

Videotapes were analysed using the OBSERVER software program (Noldus Information Technology, 1993). Frequencies of behavioural elements were recorded over 105 min during Days 1 and 2 of each trial.

The following behavioural elements were recorded for each male:

Male-to-female aggression: The male pecked a female with a downward blow of the beak, usually directed at her head. The male may also have jumped at the female, kicking at her with his feet.

Chasing females: The male ran towards a female, with or without wings raised.

Copulation: The male mounted, gripped, trod a female and appeared to achieve cloacal contact. The female often ruffled her feathers following the male's dismount.

Forced copulation: The male mounted a female and appeared to achieve cloacal contact following a struggle during which the female attempted to avoid the male. The female often squawked during the struggle.

Unsuccessful mounting: The male placed one or more feet on the female's back. No further elements of the copulatory sequence were observed due to avoidance of the female or failure of the male to copulate. There were two distinct situations where mounting did not proceed to full copulation. The first situation involved struggling by the female, resulting in her escape. The second situation involved male failure, where males failed to achieve cloacal contact, due to inappropriate orientation, slipping from the back of the female or deliberate dismounting by the male.

The following behavioural elements were recorded for females with frequencies pooled over the three females:

Interference: A female attacked or threatened the male while he was attempting to copulate with another female, disrupting the copulatory sequence.

Female-to-male aggression: A female pecked the male with a downward blow of her beak, usually directed at his head. The female may also have jumped at the male, kicking at him with her feet.

Female-to-female aggression: A female pecked another female with a downward blow of the beak, usually directed at her head. The female may also have jumped at the other female, kicking at her with her feet.

Allopecking: A female pecked gently at the comb, wattles or face of the male. Bouts of allopecking were terminated when the female engaged in a different behaviour.

2.5. Data analysis

Using SAS General Linear Means procedure (SAS Institute Inc., 1985), frequencies of behavioural events were analysed according to a repeated measures technique, in which data were arranged in arrays. Differences between treatments were determined using least-square means for mean frequencies of behavioural events during the four observation periods. Differences in behaviour between days and trials were also analysed, using orthogonal contrasts.

Since there were only 30 males reared in each treatment, males within a treatment were reared with one pen per treatment. It could be argued that this resulted in one replication of each treatment. However, housing the males individually at this stage of development would have radically affected their social behaviour and masked any treatment effects. This research examines a problem occurring in commercial conditions where group sizes are very large and we felt reducing group size below 30 individuals during rearing would compromise the application of our results. For example, the extreme aggression or mobbing at the feeder displayed by feed-restricted birds during rearing may be a contributing factor to aggression at maturity. Ideally, we would have reared nine groups of males per treatment from which an individual for testing would be selected. This was not practical or possible with the facilities available to us. Because of these limitations, we

made no attempt to quantify behaviour during the rearing period. As a compromise, males were individually housed at sexual maturity and testing began 10 weeks later. We feel that although there may have been a pen-by-treatment interaction residual from the rearing phase, the effect on behaviour 10–19 weeks later was minimal.

We were also aware of problems interpreting the results from our tests with game strain males. Since game strain males were housed and tested in a different building than were the other males, and were maintained on their breeder's feeding program, our results were confounded for both location and diet. More importantly, rearing conditions also differed, since game strain males were reared outdoors in mixed-sex, mixed-age groups. However, we were willing to work within these confounds, because we expected observations of game strain males to provide important insight into possible mechanisms of aggressiveness by broiler breeder males. We made attempts to replicate environmental conditions at the OMAFRA Isolation Unit and Poultry Research Station, with similar lighting and pen designs, and all males were tested with the same male model. Because of these confounding effects, we did not include game strain males in our statistical analysis, and comparisons between game strain males and broiler breeder or laying strain males should be interpreted with caution.

Due to technical difficulties, two LA males were not video-recorded on Day 1 during Trial 1. As a result, the standard errors for LA males on Day 1 were higher than for the other treatments.

3. Results

Mean body weights of BR, LR, LA and GA males, at 39 weeks of age, were 5.42 ± 0.12 , 2.34 ± 0.04 , 2.77 ± 0.05 and 2.11 ± 0.08 kg, respectively. Feed-restricted laying strain males were successfully maintained on a feed-restriction program equivalent to broiler breeders (North and Bell, 1990). Although the broiler breeder males were maintained on the recommended growth curve when group housed during the rearing phase, they gained weight when they were moved into individual housing. This was likely due to inadequate monitoring during weeks 21–31. At 39 weeks of age, broiler breeder males were approximately 25% above the recommended body weight (Ross Breeders, 1997).

Casual observation during the rearing phase indicated that feed-restricted laying strain males performed stereotypic pecking, mobbing behaviour at feeding time and excessive drinking. However, broiler breeder males appeared to display such behaviour with greater frequency and intensity than did laying strain males. Feed-restriction delays sexual maturity of broiler breeder males (North and Bell, 1990) and in our experiment feed-restricted laying strain males crowded and developed secondary sex characteristics later than did ad libitum fed laying strain males. Both broiler breeder and laying strain males often behaved aggressively at the feeder during rearing. However, broiler breeder males seemed more aggressive a way from the feeder, often chasing and pecking other males.

When placed with females, broiler breeder males were aggressive towards females (Fig. 1). When frequencies were averaged over the four observation periods, broiler breeder males were significantly more aggressive towards females than feed-restricted laying strain males, but not laying strain males fed ad libitum ($P < 0.02$, $P < 0.02$ and $P < 0.10$,

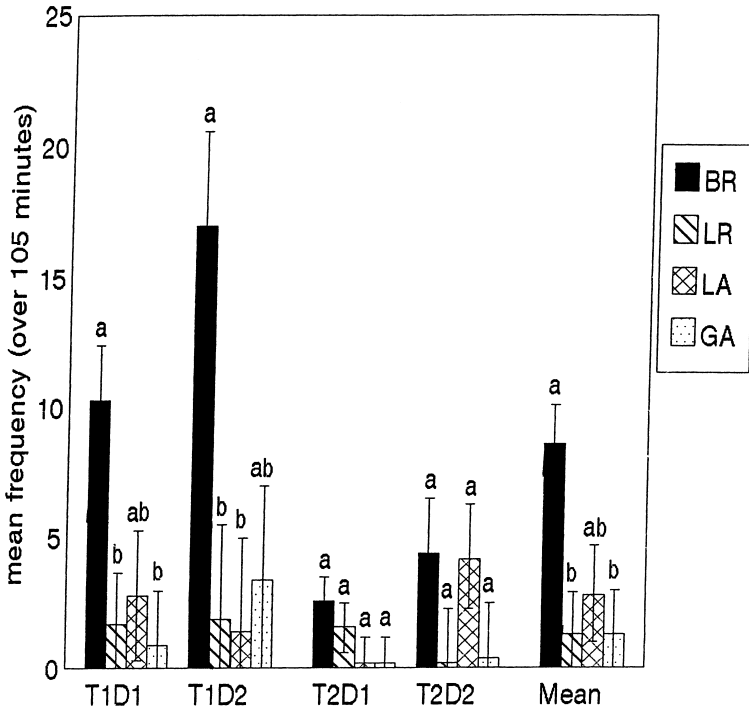


Fig. 1. Mean frequencies (\pm S.E.) of aggressive behavioural events performed by single males housed with three females during 105 min observation periods. Means with different superscripts differ significantly ($P < 0.05$). T: trial; D: day; BR: broiler breeder, feed-restricted; LR: laying strain, feed-restricted; LA: laying strain, fed ad libitum; GA: game strain, fed ad libitum.

respectively). We expected aggression to decrease over time, as the birds became acquainted, but strangely, broiler breeder males were significantly more aggressive towards females on Day 2 ($P < 0.04$). However, broiler breeder males behaved much less aggressively towards females during Trial 2 ($P < 0.0002$), at which time they did not differ from other males. Despite selection for fighting ability and motivation, game strain males displayed little male-to-female aggression. We also expected feed-restriction to increase aggressiveness of laying strain males towards females, but this did not occur.

Mean frequencies of chasing during the four observation periods were 1.3 ± 0.3 , 0.2 ± 0.3 , 0.0 ± 0.3 and 0.4 ± 0.3 for broiler breeder, feed-restricted laying strain, ad libitum fed laying strain and game strain males, respectively. Broiler breeder males chased females significantly more frequently than feed-restricted and ad libitum fed laying strain males ($P < 0.03$ and $P < 0.02$, respectively). In fact, ad libitum fed laying strain males were never seen to chase during the experiment. Chasing by broiler breeder males decreased over time, occurring significantly less often during Day 2 ($P < 0.04$) and also during Trial 2 ($P < 0.008$). Frequency of chasing by laying strain males did not significantly change over time.

Copulations were performed more frequently by laying strain males and feed-restriction did not significantly affect the frequency of copulation of laying strain males (Fig. 2).

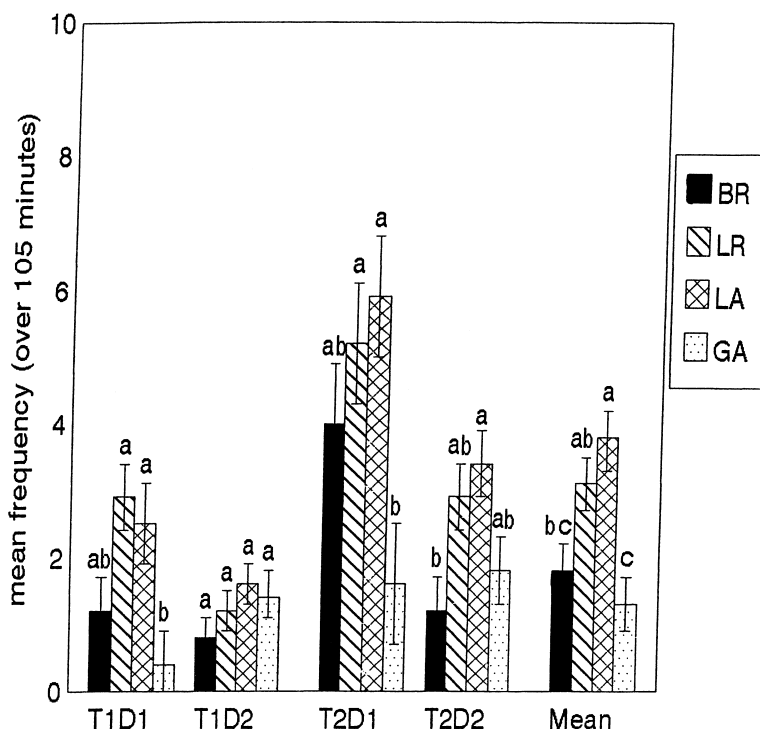


Fig. 2. Mean frequencies (\pm S.E.) of copulations performed by single males housed with three females during 105 min observation periods. Means with different superscripts differ significantly ($P < 0.05$). T: trial; D: day; BR: broiler breeder, feed-restricted; LR: laying strain, feed-restricted; LA: laying strain, fed ad libitum; GA: game strain, fed ad libitum.

Laying strain males fed ad libitum copulated more frequently than did broiler breeder males during Day 2 of Trial 2 ($P < 0.02$). Frequency of copulation decreased on Day 2, either due to fatigue or familiarity with the females ($P < 0.08$), with the exception of game strain males, who maintained a low, but steady rate of copulation during the four observation periods. Frequency of copulation by laying strain males increased during Trial 2 ($P < 0.002$), but copulation rate of broiler breeder males did not differ significantly between trials.

As fertility was not measured in this study, success of copulations could only be determined by the appearance of cloacal contact. Females rarely struggled during mating attempts of laying strain or game strain males (Fig. 3), but struggled during attempts of broiler breeder males much more frequently ($P < 0.002$). Frequencies of female struggling with broiler breeder males did not differ between Days 1 and 2, but females struggled with broiler breeder males twice as often during Trial 1 than Trial 2 ($P < 0.0001$). Male failure was also seen more frequently in broiler breeder males than in other males (Fig. 3, $P < 0.02$). Although frequencies did not differ between Trials 1 and 2, male failure by broiler breeder males occurred twice as often during Day 1 than Day 2 ($P < 0.002$) and on Day 2, broiler breeders did not differ from laying strain males fed ad libitum. Casual observation

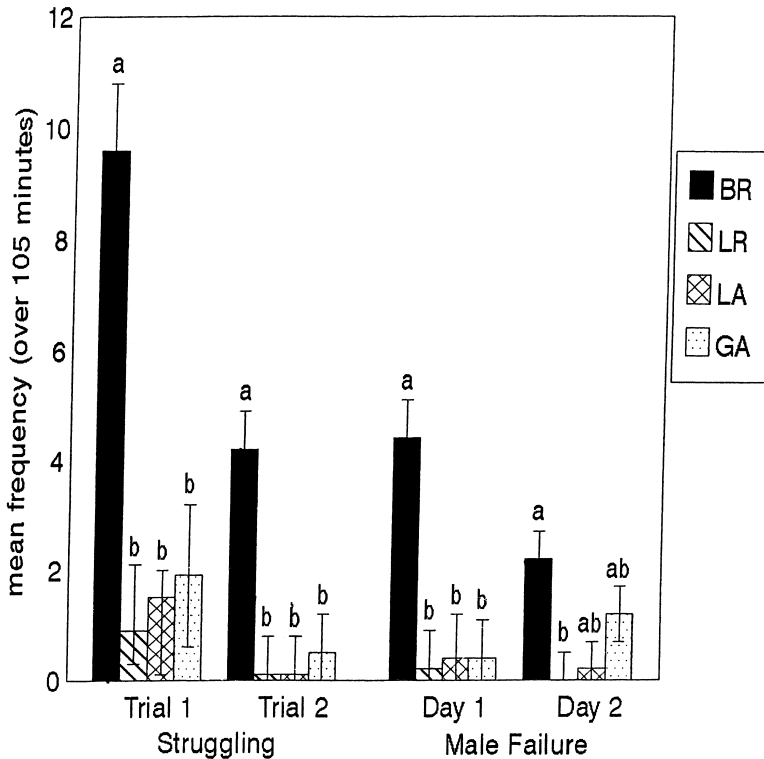


Fig. 3. Mean frequencies (\pm S.E.) of unsuccessful mating attempts performed by single males housed with three females during 105 min observation periods. Means with different superscripts differ significantly ($P < 0.05$). BR: broiler breeder, feed-restricted; LR: laying strain, feed-restricted; LA: laying strain, fed ad libitum; GA: game strain, fed ad libitum.

indicated that both game strain and broiler breeder males often attempted to mount females frontally or from the side, predisposing them to slipping from the female’s back. Laying strain males, on the other hand, performed a rear approach, to which females responded by crouching.

It was a surprise to observe females interfering with mating attempts involving other females. Interference most frequently consisted of a female running in full threat towards a copulating male, followed by a leaping attack, and females were not observed to direct aggression at the copulating female. Interference successfully disrupted copulation in some situations and females interfered with males of all strains. When averaged for the four observation periods, females interfered with copulations by broiler breeder males more frequently than by laying strain males fed ad libitum ($P < 0.05$, Fig. 4). Broiler breeder males were interfered with more than all other males during Day 1 of Trial 1 ($P < 0.02$). However, there was a decrease in the frequency of interference towards broiler breeder males between Days 1 and 2 ($P < 0.02$) so that interference by females towards males did not differ during other observation periods. Curiously, females did not interfere in aggressive

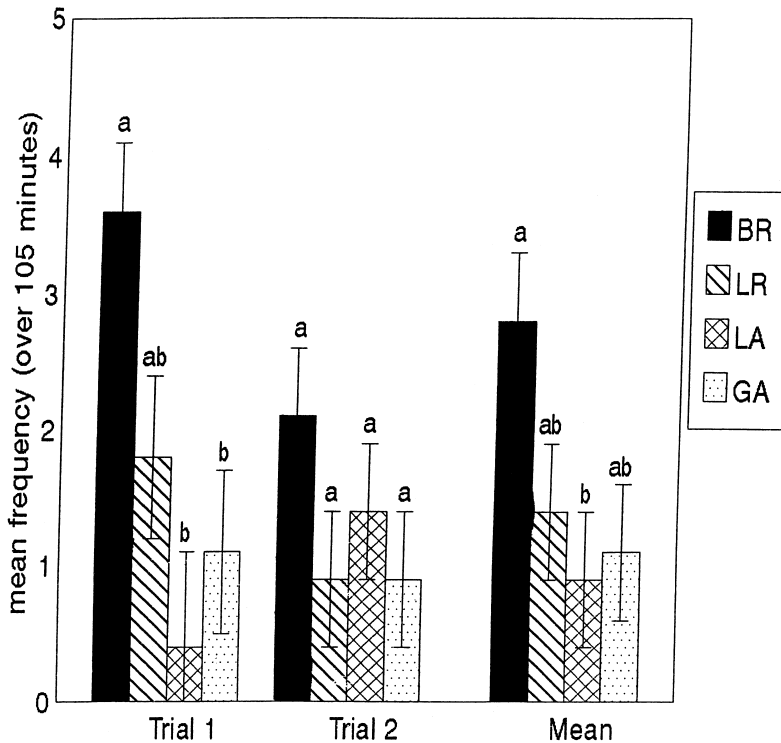


Fig. 4. Mean frequencies (\pm S.E.) of interference by three females housed with single males during 105 min observation periods. Means with different superscripts differ significantly ($P < 0.05$). BR: broiler breeder, feed-restricted; LR: laying strain, feed-restricted; LA: laying strain, fed ad libitum; GA: game strain, fed ad libitum.

interactions, either between females or between the male and other females. It is possible that squawking or struggling by the female being mated stimulated on-looking females to behave aggressively to the copulating male.

Females rarely directed aggression towards males outside the context of interference with copulation and there were no differences in frequency of female-to-male aggression between the strains. Mean frequencies (\pm S.E.) were 1.6 ± 0.9 , 0.5 ± 0.8 , 0.5 ± 0.8 and 1.7 ± 0.9 for hens housed with BR, LR, LA and GA males, respectively. Females did not appear to be either fearful of or aggressive to game strain males, as allopecks were directed towards game strain males as frequently as towards other males and very little female-to-male aggression was observed. Females performed allopecks to males of all strains (Fig. 5), but when averaged over the four observation periods, allopecks were performed more frequently to laying strain males fed ad libitum than to broiler breeder and feed-restricted laying strain males ($P < 0.05$). However, frequency of allopecking towards laying strain males fed ad libitum was significantly lower during Trial 2 than Trial 1 ($P < 0.005$) and there were no significant differences between male strains during Trial 2. Since laying strain males were very similar in appearance, regardless of rearing treatment, it is likely that

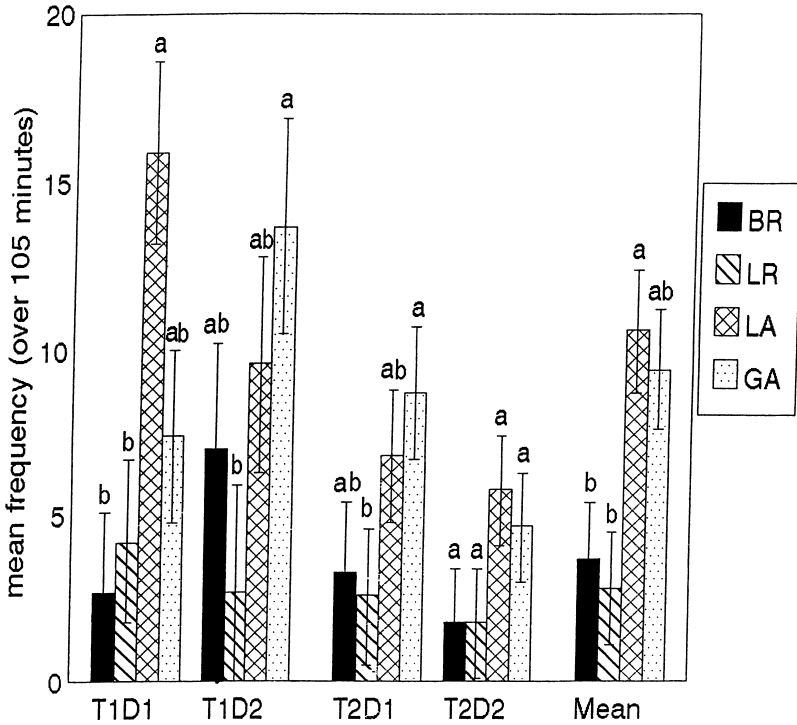


Fig. 5. Mean frequencies (\pm S.E.) of allopecking by three females housed with single males during 105 min observation periods. Means with different superscripts differ significantly ($P < 0.05$). BR: broiler breeder, feed-restricted; LR: laying strain, feed-restricted; LA: laying strain, fed ad libitum; GA: game strain, fed ad libitum.

differences in behaviour and not morphology of the males resulted in this difference in allopecking.

Aggression between females tends to be low when they are in the presence of a dominant third party, particularly when the dominant is a male (Guhl, 1949; Ylander and Craig, 1980; Bshary and Lamprecht, 1994). Hence, we used female-to-female aggression as a measure of the male's ability to maintain order within the group. There were no differences between treatments for frequencies of female-to-female aggression when frequencies were averaged for the four observation periods. However, on Day 1 of Trial 1 aggression between females was high in pens with game strain males, with frequencies of 1.1 ± 3.7 , 1.1 ± 3.7 , 0.9 ± 4.2 and 16.8 ± 3.9 for broiler breeder, feed-restricted laying strain, ad libitum fed laying strain and game strain males, respectively. Aggression between females housed with game strain males decreased between Days 1 and 2 (mean frequencies \pm S.E. were 9.6 ± 2.2 and 2.5 ± 1.5 for Days 1 and 2, respectively) and between Trials 1 and 2 (mean frequencies \pm S.E. were 9.1 ± 2.7 and 2.9 ± 0.8 for Trials 1 and 2, respectively). This raised the possibility that game strain males were unable to dominate broiler breeder females, a situation that would impact on the aggressive and sexual behaviour of these males.

3.1. Experiment 2

From Experiment 1, we determined that game strain males did not display high levels of aggression to females. However, broiler breeder females used in Experiment 1 were larger than game strain males and much larger than females of the game strain. There was also some evidence that game strain males were not able to dominate broiler breeder females adequately. We hypothesised that game strain males were as aggressively motivated towards females as were broiler breeder males, but the large size of broiler breeder females in our study inhibited the expression of aggression by game strain males. A small experiment was designed to determine the effect of male:female body size ratio on the sexual and aggressive behaviour of males.

4. Materials and methods

4.1. Treatments

A repeated measures design was used to compare the behaviour of males interacting with females of two different body sizes. Game strain males (Pine Albany) were observed interacting with small, game strain females (Asil and Pine Albany) and also with large broiler breeder strain females (Arbor Acre).

4.2. Testing

Testing in Experiment 2 involved the birds and methods from Experiment 1 with the following modifications. Males were not subjected to an aggression test prior to testing with females. A male was placed in the test pen 30 min prior to lights-out, and a single female was placed in the pen with him. Since birds were tested as male–female pairs, instead of groups of females with a single male, we were concerned about the ability of the female to escape should the male behave aggressively. A perch was provided in each pen for this purpose, but as broiler breeder females rarely perched we also included a nestbox in each pen in which she could escape if necessary. Due to the extremely flighty nature of game females, we took observations on the second evening, which allowed time for birds to become familiar with each other and the test pen. Behaviour was video-recorded from 18.00 to 20.00 h, following which the female was removed and the procedure repeated with a female of the second strain placed with the male. To account for changes in sexual motivation of the male, order of presentation of females was balanced across males. Three males were tested simultaneously and males were tested with the same individuals as neighbours. All females were sexually inexperienced and each female was tested with only one male. Males had received limited sexual experience during Experiment 1. All tests were performed during 1 week, when birds were approximately 40 weeks of age. Mean body weight of game strain males was 2.1 ± 0.1 kg at 40 weeks of age, whereas the mean (\pm S.E.) body weights of game strain females and broiler breeder females were 1.4 ± 0.1 and 3.6 ± 0.2 kg, respectively.

4.3. Behavioural observations

As in Experiment 1, behaviour was analysed using the OBSERVER software program (Noldus Information Technology, 1993) and frequencies and durations of behaviour were recorded over 105 min. In addition to behavioural elements described in Experiment 1, frequencies of courtship displays (Wood-Gush, 1954) were also recorded.

4.4. Data analysis

Since the behavioural elements of interest occurred only as rare events and since Experiment 2 involved only one observation period per treatment, the data set contained many zero values. Consequently, non-parametric statistical analysis was performed using the SAS NPAR1WAY procedure (SAS Institute Inc., 1985). The Kruskal–Wallis test on Wilcoxon Scores of ranked sums was used to determine differences between female strain treatments and between Days 1 and 2.

5. Results

Game strain males did not behave aggressively towards females and no overt aggression was displayed towards females of either strain. However, there were differences in the behaviour of game strain males towards females of the two strains. Pecking of females was more often directed at broiler breeder females ($P < 0.02$), but occurred only at low frequencies (Fig. 6). Chasing was also rare (Fig. 6), and was performed more frequently to game strain females ($P < 0.02$). Chasing appeared to be stimulated by the behaviour of game strain females, since males chased females when they ran or flew down from perches.

Since copulation frequency did not differ between Days 1 and 2, males were not becoming fatigued when the second female was presented on Day 2. Males copulated more frequently with broiler breeder females (Fig. 6, $P < 0.02$) and this seemed to be most affected by difference in the behaviour of the females. Broiler breeder females appeared to be highly motivated to mate and often crouched prior to courtship by the male. They also spent more time in close proximity to the male and performed significantly more allopecking to his comb and wattles than did game strain females (Fig. 6, $P < 0.02$). In contrast, game strain females avoided males and were not as accessible for copulation due to perching. Unsuccessful mounting occurred as frequently with game strain females as with broiler breeder females (mean frequencies \pm S.E. were 0.3 ± 0.3 and 0.8 ± 0.3 , with game strain and broiler breeder strain females, respectively, $P > 0.10$). However, mounts were longer in duration when performed with game strain females (mean durations \pm S.E. were 6.7 ± 1.0 and 1.9 ± 1.3 s, with game strain and broiler breeder strain females, respectively, $P < 0.04$). Males may have experienced more difficulty mating with game strain females, since their prior experience had been with the large broiler breeder females. Forced copulations did not occur with females of either strain.

Males performed waltzing as frequently to females of either strain, suggesting that female strains did not differ as releasers of aggressive and sexual motivation (mean frequencies \pm S.E. were 6.5 ± 2.3 and 3.5 ± 2.3 , with game strain and broiler breeder strain

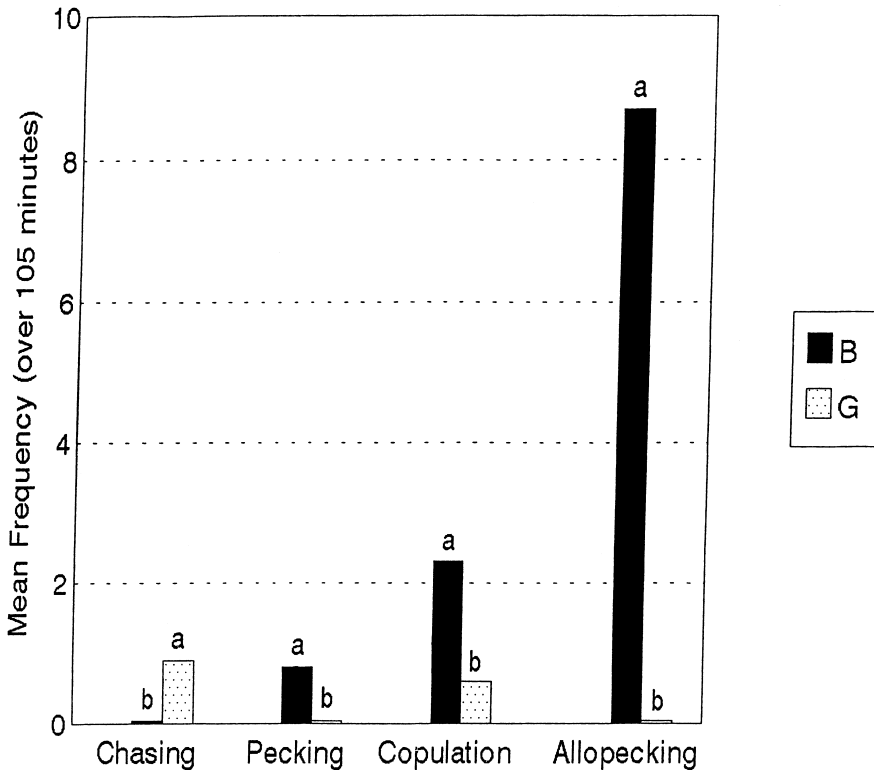


Fig. 6. Mean frequencies (\pm S.E.) of chasing, pecking and copulation performed by single game strain males and mean frequencies (\pm S.E.) of allopecking performed by single broiler breeder and game strain females during 105 min observation periods. Means with different superscripts differ significantly ($P < 0.05$). BR: broiler breeder, feed-restricted; LR: laying strain, feed-restricted; LA: laying strain, fed ad libitum; GA: game strain, fed ad libitum.

females, respectively, $P > 0.10$). However, wing-flapping by males occurred most frequently when they were housed with game strain females (mean frequencies \pm S.E. were 64.3 ± 7.1 and 39.6 ± 7.1 , with game strain and broiler breeder strain females, respectively, $P < 0.02$) and males wing-flapped twice as frequently on Day 1, regardless of treatment (mean frequencies \pm S.E. were 68.7 ± 7.1 and 35.3 ± 7.1 , with Days 1 and 2, respectively, $P < 0.02$). Wing-flapping was rarely performed by females of either strain and no strain differences were detected.

6. Discussion

Our first hypothesis was that feed-restriction during the rearing phase would increase aggressiveness of males towards females. The results from this study indicate that this was not the case. Feed-restriction during rearing delayed sexual maturity, but sexual behaviour

and aggression towards females did not differ at maturity from laying strain males fed *ad libitum*. However, we did not measure aggression displayed at the feeder and it is possible that feed-restricted males display high levels of aggression in the context of feeding. It is also possible that there is an interaction between genetic strain and effects of feed-restriction. Since broiler breeder fowl have been selected for rapid growth and large appetites, it seems likely broiler breeder males experience greater suffering from hunger associated with feed-restriction than do laying strain males. It is, therefore, possible, but unlikely, that feed-restriction may lead to increased aggression in broiler breeder males, but not in laying strain males.

It was also our hypothesis that broiler breeder and game strain males would behave more aggressively towards females than would laying strain males. We found broiler breeder males to behave aggressively towards females, through overt aggression and rough sexual behaviour, but game strain males did not. Conversely, game strain males displayed extremely high levels of aggressiveness when presented with a male model in an earlier experiment, whereas broiler breeder males did not (Millman and Duncan, 2000). Hence, it would appear that aggressiveness towards females does not result from a general increase in aggressive motivation.

So if broiler breeder males are not behaving aggressively towards females as a result of a general increase in aggressive motivation, why are they displaying this behaviour? There would seem to be several possible explanations. First, aggression may result from problems of social dominance. Although males may display overt aggression towards females immediately following mixing, aggression should decrease as social dominance is established (Wood-Gush, 1955; Guhl, 1961; Collias et al., 1966). However, aggression towards females by broiler breeder males increased during Day 2. This raises the question, were broiler breeder males able to dominate females adequately? Dominance of the male over the female is believed to facilitate mating (Guhl, 1949; Wood-Gush, 1954, 1956) and broiler breeder and game strain males in our study copulated significantly less frequently than laying strain males. However, aggression between females should decrease in the presence of a dominant third party (Craig and Bhagwat, 1974; Ylander and Craig, 1980; Bshary and Lamprecht, 1994), and female-to-female aggression was low in pens with broiler breeder males. It is more likely that game strain males experienced difficulty dominating broiler breeder females, but they did not behave aggressively towards them in either Experiment 1 or 2. Hence, we suggest that aggression towards females by broiler breeder males is not a problem of social dominance.

Second, it is also possible that females behave in a way that stimulates broiler breeder males to behave aggressively towards them. Broiler breeder females appeared fearful of broiler breeder males, but not laying strain or game strain males. Since broiler breeder males behaved more aggressively towards females than other males did, it is not clear if females were responding to aggressive behaviour directed towards them. It is possible that the large size of the broiler breeder males stimulated fearfulness in broiler breeder females. In Experiment 2, game strain females were smaller than game strain males and also appeared fearful of game strain males, while broiler breeder females did not. Game strain males were not observed to display overt aggression to females of either strain, but as observations were not performed on Day 1 in Experiment 2, it is possible that males behaved aggressively to game strain females before observations were taken. However,

Experiment 2 did not have a proper control for the extreme flightiness of game strain females. Game strain females were very fearful of human handlers, becoming quite hysterical when they were fed or their pens cleaned, and so, it is possible they would have equally avoided small males or even unfamiliar females. Conversely, broiler breeder females displayed little fear of handlers, and seemed inherently curious, approaching and pecking at boots and hands. Hence, it is likely that aggression by broiler breeder males preceded avoidance by females, and that females learned to be fearful of broiler breeder males.

Third, it is possible that aggression towards females results from difficulty broiler breeder males experience when mating. Selection for meat traits may impose limitations on the mating ability of broiler breeder males. Our results support the hypothesis that broiler breeder males experience more difficulty mating, since unsuccessful mounts were much more frequently performed by broiler breeder males. The large size of broiler breeder males allows them to force copulations on unwilling females, but also makes it difficult to achieve cloacal contact. Duncan et al. (1990) found that low fertility of older broiler breeder flocks resulted from inability of males to achieve cloacal contact rather than declining libido. Breast angle also likely affects the ability of high breast yielding males to achieve cloacal contact (Wilson et al., 1979; Fontana et al., 1990; Hocking and Bernard, 1997). Although difficulty mating could account for lacerations which often occur along the torso of broiler breeder females in commercial situations, it does not explain the high incidence of aggressive pecks by broiler breeder males occurring outside a mating context.

Fourth, it is possible that broiler breeder males behave aggressively towards females as a result of sexual frustration associated with mating difficulties. Frustration resulting from thwarting of feeding behaviour has been shown to increase aggression towards females by Leghorn males (Duncan, 1970). Males perform more wing-flapping, indicative of frustration, when males can interact with, but not mate with females (Duncan, 1970). In Experiment 2, game strain males wing-flapped more with game strain females than broiler breeder females. Since game strain females avoided males and did not copulate, it is likely that these males were sexually frustrated. However, game strain males did not behave aggressively towards females. Game strain males also wing-flapped more on Day 1 regardless of female strain, suggesting that wing-flapping may more accurately reflect increased arousal or conflict resulting from changes to social and physical environment. Hence, there was no clear evidence that sexual frustration resulted in increased aggression towards females or that broiler breeder males were experiencing higher levels of sexual frustration than males of other strains.

Finally, struggling of females during mating may release aggressive behaviour by males. There was some evidence that struggling by females released aggression in other females, which was directed at the copulating male. However, it is difficult to know if struggling by females is a causal mechanism of, or a result of, aggressive male behaviour. Females rarely resisted mating attempts of laying strain or game strain males, but frequently terminated mating attempts of broiler breeder males. It is possible that large body weight and struggling to achieve cloacal contact may make copulation with broiler breeder males painful to females. However, if females were learning to avoid pain associated with mating, one would expect avoidance and struggling by females to increase over time. This did not

occur, and hence, pain during mating cannot adequately explain why females struggle and why males are aggressive towards them.

A more likely explanation is that struggling by females occurs because broiler breeder males do not stimulate sexual motivation of females. Broiler breeder females solicited copulations with laying strain males in Experiment 1 and with game strain males during Experiment 2. Although not recorded here, our previous research indicated that broiler breeders displayed little courtship behaviour when compared with laying strain males (Millman et al., 1996). Differences in courtship displays, particularly tidbitting, which is highly attractive to females, may have accounted for the high frequency of approach by females to displaying laying strain males. Allopecks were performed less often to broiler breeder males, which may have reflected increased fearfulness of males by females or that females found broiler breeder males less attractive.

In conclusion, aggressiveness towards females appears to be a problem specific to male broiler breeder strains. This experiment does not support the hypothesis that aggression towards females is associated with a general increase in aggressiveness in broiler breeder male strains. Secondly, the hypothesis that aggression towards females results from frustration associated with severe feed-restriction of broiler breeder fowl is also unsubstantiated. Lastly, there is no clear evidence that aggression towards females decreases with sexual experience or familiarity with individual females.

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