EDUCATION AND PRODUCTION

Male Broiler Breeder Fowl Display High Levels of Aggression Toward Females

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ABSTRACT Commercial broiler breeder males are reported to display high levels of aggression, often injuring and sometimes killing females. Aggression toward females by mature male domestic fowl is rare and may be regarded as aberrant behavior. The objective of this study was to determine the effects of genetic strain and feed restriction on the sexual and aggressive behavior of male domestic fowl. A 3 × 2 factorial design was used to compare the behavior of three genetic strains (two broiler breeder strains and one commercial laying strain) on two feeding regimens (one restricted and one fed ad libitum) between 25 and 37 d of age. At 22 wk of age, pairs of same-strain males were penned with 20 females of a broiler breeder strain. Behavior was sampled from each pen for six 10-min periods during Weeks 25, 27, 29, 33, and 37. Broiler breeder males displayed significantly more male-to-male ($P < 0.0197$) and male-to-female aggression ($P < 0.0005$) than laying strain males. Broiler breeder males chased females ($P < 0.0001$), forced more copulations ($P < 0.0003$), and displayed little courtship behavior ($P < 0.0001$) compared with laying strain males. There were no behavioral differences between broiler breeder strains. It was expected that feed restriction would result in increased aggression. However, males fed ad libitum displayed the most male-to-male ($P < 0.0035$) and male-to-female ($P < 0.0273$) aggression. Sexual behavior was not affected by feeding regimen. In conclusion, broiler breeder males display aberrant sexual behavior and extremely high levels of aggression, which are associated with genetic differences, not feed restriction.

(*Key words*: aggression, broiler breeder chicken, sexual behavior, feed restriction, genetics)

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INTRODUCTION

This investigation arose from concerns raised by the poultry industry regarding high levels of aggression displayed by broiler breeder males (Dr. Rachel Ouckama, veterinarian, 1997, Curtis Chicks, Port Hope, Ontario L1A 3V5, personal communication). Males have been reported to behave aggressively toward females, injuring and sometimes killing them (Mench, 1993; Brake, 1998). Results from an informal survey of broiler breeder producers in Southern Ontario (Millman, 1999) suggest that where aggressive males are a problem, hens tend to remain on raised slatted areas and often have severe lacerations on the back of the head and along the torso, beneath the wings. Males have also been reported to display high levels of aggression toward human handlers. Outbreaks of aggression are sporadic and do not occur consistently on the same farm. Male aggression toward females peaks at 5 wk following mixing, and males continue to behave aggressively throughout the life of the flock, causing problems of low fertility and high hen mortality. Although aggression can be expected when mixing unfamiliar birds, aggression by mature males toward females is unusual (Wood-Gush, 1956, 1958a; Kruijt, 1964; Craig and Bhagwat, 1974; Ylander and Craig, 1980; Rushen, 1983/84; Bshary and Lamprecht, 1994). Males and females have separate social hierarchies, and males dominate females passively (Guhl, 1949).

Problems of male aggression could have arisen as a result of feed restriction. Frustration resulting from feed deprivation has been shown to increase aggressiveness of caged laying strain chickens, including increases in male-to-female aggressive pecks (Duncan and Wood-Gush, 1971). Feed-restricted broiler stock peck and threaten more frequently than those fed ad libitum during the rearing period (Mench, 1988; Shea et al., 1990). Much of this aggression occurs at the feeder and likely results from frustrated feeding behavior of hungry birds. Savory et al. (1993b) found that broiler breeders feed-restricted according to management guidelines were three times as motivated to eat compared with birds fed ad libitum that were deprived of food for 72 h. Furthermore, motivation to eat was as great following consumption of the daily

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Abbreviation Key: A = group fed ad libitum; B1 = broiler breeder 1 strain (Peterson); B2 = broiler breeder 2 strain (Ross); L = laying strain (ISA Brown); R = feed-restricted group.

ration as it was prior to feeding. Oral stereotypies suggestive of a high level of frustration, such as spot pecking, occur at high frequencies in broiler breeders under severe feed restriction, but are virtually absent in birds fed ad libitum (Hocking et al., 1996). It is possible that the advantages of controlling male body weight with separate-sex feeding have resulted in more severe feed restriction than was previously possible with combined feeding systems. Such levels of feed deprivation may have also resulted in the manifestation of high levels of aggression in broiler breeder males.

There is also some evidence that the problem of male aggression may be genetic in origin. Initial reports from the poultry industry associated the problem with one particular parent strain and corresponded with the introduction of high breast-yielding lines. Male aggression is now being reported in all commercial broiler breeder strains. Aggression toward females does not appear to be a problem in commercial layer breeder stocks, nor in lighter-body weight broiler breeder stocks (Brake, 1998). It is possible that through attempts to select males for sexual vigor, inadvertent selection for sexual aggression has occurred. Selection of divergent lines has successfully demonstrated a genetic component of mating ability (Wood-Gush, 1960; Siegel, 1972). Similarly, experiments have indicated a genetic basis of male-to-male aggressiveness in domestic fowl (Siegel, 1959; Craig et al., 1975; Marsteller et al., 1980). Wood-Gush (1958b) found no significant difference between high and low mating lines in a male-to-male aggression test, but observed that males in the low mating line were more aggressive toward females. It is possible for aggression toward females to have arisen in the broiler parent stock either through direct or indirect selection, or as a result of genetic drift from the inbreeding of foundation lines.

The objective of this study was to determine the effects of genetic strain and feed restriction on the sexual and aggressive behavior of male domestic fowl. This experiment also provided an opportunity for ethological analysis of apparently aberrant mating behavior in broiler breeder fowl.

MATERIALS AND METHODS

Treatments

This experiment was designed as a factorial with three genetic strains and two feeding regimens, for a total of six treatments. A broiler breeder strain (B1 = Peterson) was compared with a broiler breeder strain reputed to display high levels of aggression (B2 = Ross). A commercial laying strain (L = ISA Brown) acted as a control. At sexual maturity, males of all treatments were feed-restricted (R) or fed ad libitum (A). All males were housed with broiler breeder females of the Arbor Acre strain. Females were feed-restricted in all treatments. Because only two rooms were available to us, with six pens per room, this experiment was divided into three trials for a total of six complete replications of the six treatments.

Birds

Rearing Phase. All birds were obtained from local hatcheries as 1-d-old chicks, were vaccinated against local diseases, and were given a coccidiostat. Male broiler breeder chicks were toe-trimmed (claw of the first digit) and had combs dubbed at the hatcheries. Chicks were reared in single-sex groups of 20 to 30 individuals with visual and auditory contact between pens. Pine shavings were used as litter. At 1 wk of age, daylength was reduced to 8 h of light:16 h of dark and was provided at an intensity of 10 lux. All chicks were beak-trimmed at 7 d of age to prevent feather pecking.

A starter ration (Leeson and Summers, 1991) was provided ad libitum for the first 7 d, after which a grower ration (Leeson and Summers, 1991) was provided. Because laying strain males are not normally feed-restricted, males of this strain were fed ad libitum throughout the rearing period. Broiler breeder males and females were feed-restricted according to the management guidelines for each strain. At 11 wk of age, a skip-a-day feeding regimen was adopted to maintain flock uniformity. Body weight was recorded weekly for males of all strains and for a random sample of females.

Experimental Conditions. At 22 wk of age, pairs of same-strain males with average body weight and good feet and leg conformation were placed in 3.6 × 3.6-m pens with 20 randomly chosen females. Treatments were randomized to pens according to a Latin Square design with one complete replication of treatments per room. Males were fed from raised hoppers, with feed provided ad libitum (A) or restricted (R) according to management guidelines for each strain. Because laying strain males are not normally feed-restricted, we restricted feed for the LR treatment such that the males remained at 75% of the body weight of LA treatment males. This percentage was chosen so that LR males would be hungry, but fertility and reproductive functions would not be compromised. Females were fed a laying ration (Leeson and Summers, 1991) from troughs containing male exclusion grills, and feed was restricted according to the management guidelines for the Arbor Acres strain. Due to their smaller size, laying strain males were able to squeeze their heads through the exclusion grills and feed from the females' troughs. For this reason, all males were fitted with Nozbonz,™ which successfully facilitated separate-sex feeding (see Ethical Note). Water was not restricted.

Pens were provided with nest boxes and pine shavings for litter. Visual contact between pens was prevented by wooden partitions to a height of 1.2 m. At 22 wk of age, daylength was increased to 16 h daily, with lights on at 0500 and off at 2100. Birds were fed at 0900, and eggs were collected daily.

Behavioral Observations

Direct observations were taken on 6 consecutive days during Weeks 25, 27, 29, 33, and 37. These weeks were chosen because it was expected that aggression by males

toward females would be greatest 5 wk following mixing (see Introduction), and to avoid confounding effects of mating difficulties experienced by older males. On weeks when observations were taken, eggs from each pen were incubated and candled at 14 d to determine fertility. Observations were taken from a step ladder outside each pen, which allowed for a panoramic view of the pen. After allowing 2 min for birds to habituate to the observer's presence, frequencies of behavior for both males were recorded over 10 min. General responses of females to male displays were also recorded. The order of pens observed was randomized as a Latin Square over 6 d each week. Observations were taken either prior to feeding (0600 to 0830), after feeding (1130 to 1400), or prior to lights-out (1800 to 2030), with time of observation randomized over the 6-d period.

Descriptions of behavioral elements recorded were as follows:

Male-to-male aggression:
The male chased, pecked, or jumped at the other male in the pen.

Pecking females:
The male struck a female with a downward blow of the beak, usually directed at her head.

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

Copulation:
The male mounted, gripped, and trod a female and appeared to achieve cloacal contact. The female ruffled her feathers following the male's dismount. Copulations included both forced copulations (see below) and those in which the female did not struggle or squawk during the copulatory sequence.

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.

Mounting:
The male approached a female and placed one or more feet on her back. The female avoided the male, and no further elements of the copulatory sequence were observed.

Tidbitting:
A courtship display was performed, in which the male repeatedly pecked at the ground with his beak, with or without ground-scratching with his feet. Food calls were often emitted, but were not recorded due to difficulty in identifying the individual producing the call within the room.

High step advance:
A courtship display was performed, in which the male approached the female with a strutting walk. The legs were lifted and extended forward in an exaggerated manner.

Waltzing:
A display was performed, occurring in courtship and aggressive situations, in which the male approached the female in a sideways or circling path with his far wing lowered. His head was usually lowered and his feet made a rasping sound as they passed through the primary feathers of the wing.

Crowing:
A stereotyped vocalization was emitted as the male maintained an upright posture.

Wing-flapping:
A display was performed, occurring in varying levels of intensity, in which wings were clapped together while the male was in an upright posture. In a less intense form, wings were clapped together while the head and body of the male remained level.

Avoidance by females:
The male's behavior resulted in a female running away from him.

Approach by females:
The male's behavior resulted in one or more females walking or running toward him.

Data Analysis

This experiment was conducted as a 3×2 factorial, repeated-measures design, with genetic strain and feeding regimen as factors. Frequencies of behavior were analyzed according to a repeated-measures technique, with arrays across weeks, using the SAS general linear models procedure (SAS, 1985). Because we were interested in behavior occurring as rare events, our data set contained many small numbers and zero values. To address this problem, we summed the six observation periods per week and performed our statistical analysis on the weekly totals. Weekly means and linear contrasts over weeks were analyzed using the least squares means procedure, with strain and feed restriction as main effects of the model. Differences between broiler breeder strains and the laying strain were investigated as orthogonal contrasts, as were linear contrasts over weeks.

Ethical Note

1) Our experimental protocol was approved by the University of Guelph Animal Care Committee under the guidelines of the Canadian Council of Animal Care.

2) Nozbonz™ are small plastic pegs pushed through the septum of the beak. There was a small amount of blood (approximately one drop) observed in one or two males of each strain when the Nozbonz™ was placed in the septum. Although the procedure was probably painful, we observed that the males immediately commenced foraging once the Nozbonz™ were fitted, and they did not appear to affect behavior of the males.

3) Behavior of all strains of feed-restricted birds indicated high levels of hunger and frustration. However, the levels fed were in accordance with those of the broiler breeder industry and, hence, were required to replicate commercial conditions and to prevent confounding effects of obesity in the broiler breeder strains.

RESULTS

To make detailed behavioral observations, small group sizes were necessary to allow for identification of individual birds. It was anticipated that small group sizes might preclude the extreme aggression observed in commercial settings, where typically 5,000 to 10,000 birds per floor are housed. However, these concerns proved to be unfounded; high levels of aggression were observed in the experimental conditions. In pens where males were particularly aggressive, females were "corralled" or huddled in corners of the pen. Males would grip females by the comb and pull them from the group. Chasing and pecking of the stray female often followed. Whether this behavior was an attempt to mate with an unwilling female or resulted from aggressive motivation was not clear. Extreme aggression such as this never occurred in pens with laying strain males. In the final weeks of the experiment, a small number of females were severely injured and were replaced with inexperienced females. Casual observation indicated that broiler breeder males did not react differently to inexperienced or experienced females. Injuries incurred by females were similar to those reported in commercial flocks, with lacerations along the torso, beneath the wings, and on the back of the head.

Broiler breeder males showed much higher levels of aggression than laying strain males in all categories measured, and the two broiler breeder strains were not found to differ significantly from each other (Figure 1). The frequency of male-to-male aggressive acts was significantly greater in broiler breeder strains ($P < 0.02$). The high level of aggression that broiler breeder males directed at females was particularly surprising. Pecking and chasing of females were extremely rare with laying strain males. In comparison with laying strain males, broiler breeders displayed five to ten times more pecking ($P < 0.0005$) and chasing ($P < 0.0001$). Females appeared to be fearful of broiler breeder males, running away from the B1 strain in particular ($P < 0.05$).

In accordance with reports from the poultry industry, broiler breeder males were also found to be rough during mating. Although the copulation rate did not differ between strains (Figure 2), approximately 50% of the copulations performed by broiler breeder males were forced copulations ($P < 0.0003$). Casual observation indicated that females housed with broiler breeder males rarely adopted a sexual crouch, and copulations usually occurred after a chase. Broiler breeder males also performed more unsuccessful mating attempts, mounting females significantly more frequently than laying strain males ($P < 0.004$). However, males of the two broiler breeder strains did not differ from each other. During these mating attempts, mounting did not proceed to full copulation due to either the inability of males to achieve cloacal contact or successful escape attempts of unwilling females. Percent fertility was highest in pens with laying strain males ($P < 0.02$). Surprisingly, there was no significant interaction between feeding regimen and genetic strain; nor did feeding regimen significantly affect percentage fertility (Table 1). Percentage fertility did not significantly change between weeks for any of the strains. Fertility was lower than expected, probably because of avoidance of males by females that were housed with aggressive broiler breeder males.

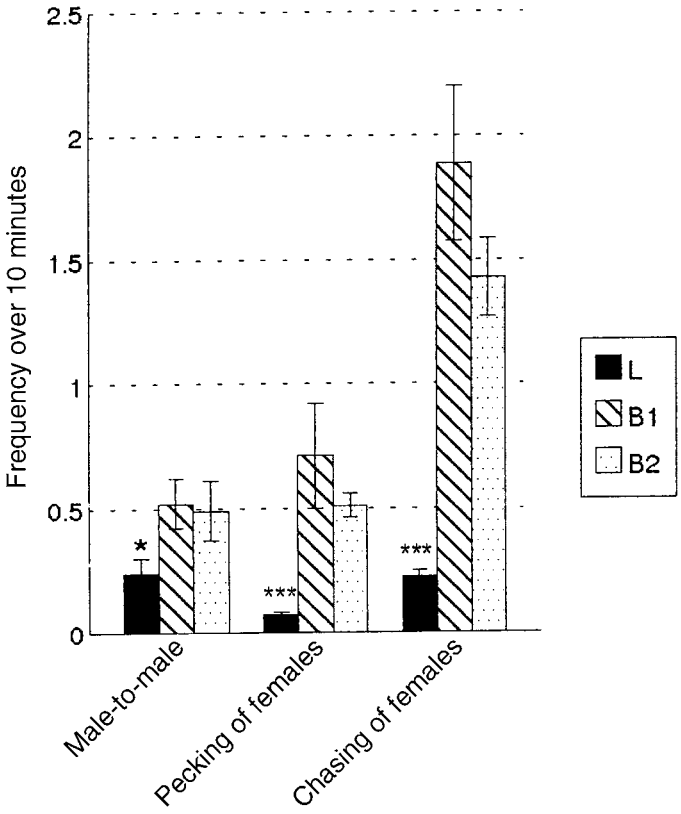

FIGURE 1. Effects of genetic strain on mean frequencies of aggressive behavioral events during 10-min observation periods for all weeks combined. L = laying strain males (ISA Brown), B1 = broiler breeder 1 strain males (Peterson), B2 = broiler breeder 2 strain males (Ross).

Courtship displays are important elements of sexual behavior of the domestic fowl, and broiler breeder males were found to show deficiencies in courtship behavior compared with laying strain males (Figure 3). Laying strain males performed tidbitting twice as frequently as did broiler breeder strains ($P < 0.0001$). Similarly, laying strain males displayed high step advance much more frequently than did broiler breeder males ($P < 0.0001$). It is interesting that the frequency of waltzing, a display occurring in both sexual and aggressive contexts, did not differ significantly between strains and occurred at low levels in laying strain males relative to tidbitting and high step advance displays. Females were found to approach laying strain males much more frequently than broiler breeder males ($P < 0.0001$). Tidbitting is highly attractive to females and may have accounted for the difference in responses of females. The two broiler breeder strains did not differ from each other in any of the courtship elements.

Feed restriction significantly reduced body weight in all strains, as was expected. When behavioral observation commenced at 25 wk of age, B1A and B1R males weighed

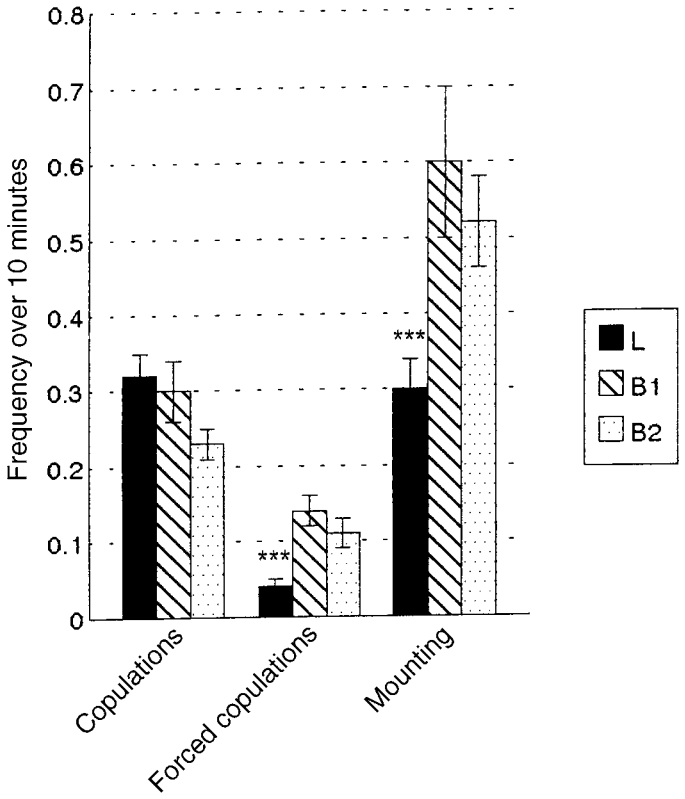

FIGURE 2. Effects of genetic strain on mean frequencies of copulatory behavioral events during 10-min observation periods for all weeks combined. L = laying strain males (ISA Brown), B1 = broiler breeder 1 strain males (Peterson), B2 = broiler breeder 2 strain males (Ross).

4.47 ± 0.11 kg and 3.33 ± 0.11 kg, B2A and B2R males weighed 4.27 ± 0.14 kg and 3.76 ± 0.23 kg, and LA and LR males weighed 2.29 ± 0.05 kg and 1.96 ± 0.07 kg, respectively. Body weights of feed-restricted broiler breeder males were similar to industry recommendations of 3.27 to 3.45 kg for cockerels at 24 wk of age (North and Bell, 1990). At 37 wk of age, B1A and B1R males weighed 5.48 ± 0.07 kg and 4.50 ± 0.09 kg, B2A and B2R males weighed 5.58 ± 0.22 kg and 4.45 ± 0.11 kg, and LA and LR males weighed 2.69 ± 0.08 kg and 2.38 ± 0.04 kg, respectively. Broiler breeder males with feed provided ad libitum were not extremely obese, probably because all males were feed-restricted during the rearing phase. Surprisingly, feed restriction did not increase the aggressiveness of males, either toward males or toward females.

TABLE 1. Mean percent fertility (± SE) of eggs collected during Weeks 27 to 37

Factor	% Fertility
Breed	
Laying strain	93.4 ± 0.8[a]
Broiler, Strain 1	79.0 ± 5.1[b]
Broiler, Strain 2	80.2 ± 4.6[b]
Feeding condition	
Ad libitum	81.1 ± 3.4[b]
Restricted	87.3 ± 3.4[a]

[a,b]Within category, means with different letters are significantly different ($P < 0.05$).

In fact, males fed ad libitum were found to be much more aggressive (Figure 4) regardless of strain. Male-to-male aggression was twice as frequent in the ad libitum-fed than in the restricted-fed treatment ($P < 0.0035$). Ad libitum-fed males were also twice as aggressive toward females, as measured through pecking ($P < 0.03$) and chasing ($P < 0.005$).

Waltzing was performed twice as frequently by ad libitum-fed than by restricted-fed males (mean frequency during 10 min was 0.54 and 0.26, respectively: $P < 0.0001$), whereas the courtship displays of tidbitting and high step advance did not differ. No differences resulting from feeding regimen were found in frequencies of copulation, forced copulation, or mounting, indicating that feed restriction did not affect the sexual motivation of males. Lack of cloacal contact has been associated with reduced fertility in older broiler breeder males (Duncan et al., 1990); however, fertility was not affected by feeding regimen in our study, despite obesity of broiler breeder males fed ad libitum (see above). However, males were only observed for the first half of a normal breeding season. Crowing occurred twice as frequently in ad libitum-fed than in restricted-fed males (mean frequencies during 10 min were 2.09 and 0.94 respectively; $P < 0.0001$). Similarly, wing-flapping occurred twice as frequently in ad libitum-fed than in restricted-fed males (mean frequencies during 10 min were 1.50 and 0.70, respectively; $P < 0.0001$).

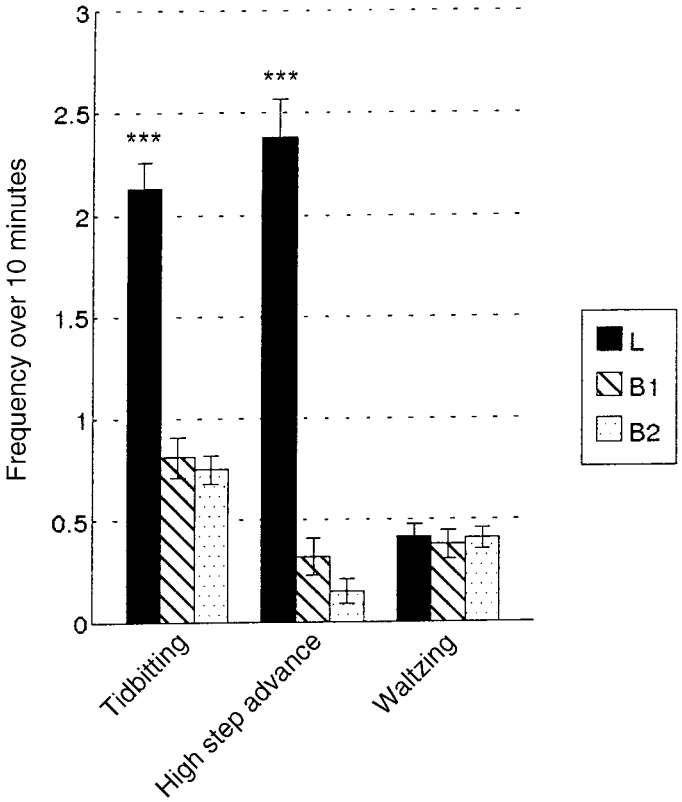

FIGURE 3. Effects of genetic strain on mean frequencies of courtship behavioral events during 10-min observation periods for all weeks combined. L = laying strain males (ISA Brown), B1 = broiler breeder 1 strain males (Peterson), B2 = broiler breeder 2 strain males (Ross).

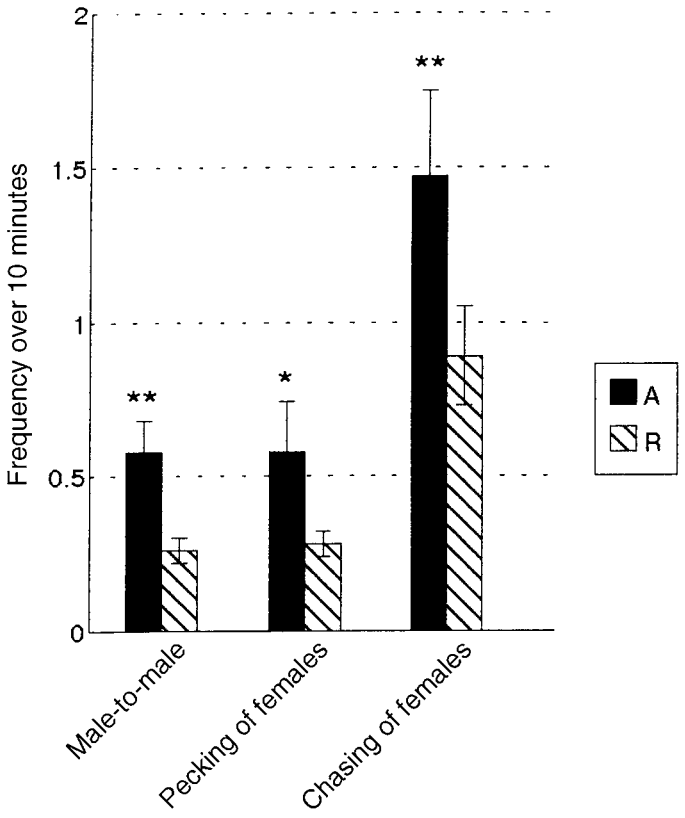

FIGURE 4. Effects of feeding regimen on mean frequencies of aggressive behavioral events during 10-min observation periods for all weeks combined. A = males fed ad libitum, R = feed-restricted males.

Because observations commenced several weeks following mixing, it was expected that differences in aggressive and sexual behavior would not be accounted for by differences in learning or maturity. No significant differences were found in the linear contrast over time for any of the behavior elements, with the exception of crowing ($P < 0.004$), which decreased over time in the ad libitum-fed treatment. Consequently, if the males learned to act aggressively in response to females, or learned to perform courtship displays, this must have occurred during the first weeks following mixing and before behavioral observations were taken. Because differences in behavior resulting from strain and feeding regimen persisted over time, obesity was unlikely to be a causative factor in the differences of aggression and sexual behavior.

DISCUSSION

The results of this experiment indicate that broiler breeder males display differences in aggressive and sexual behavior compared with laying strain males. These differences may be related, or they may represent two distinct problems. Broiler breeders performed more male-to-male and male-to-female aggressive interactions than laying-strain males. Male-to-female aggression refers to situations in which no noticeable sexual elements were involved. Pecks to the head with a downward motion of the beak, frontal leaping, and sparring behavior may be considered as male-to-female aggression. Sexual aggression refers to situations in which mating behavior is mixed with aggressive elements. Forced copulations, chasing, gripping and pulling the comb, leaping on a hen's back, and pecking while mounted on a hen may all be considered elements of sexual aggression.

Sexual aggression is aberrant behavior in mature domestic fowl and should be of concern to the poultry industry for reasons of economics and reduced animal well-being. Injuries that hens incurred in this experiment were severe and corresponded with those reported in commercial conditions. Because lacerations occurred at the back of the head and along the torso, it can be concluded that injuries resulted from sexual aggression rather than male-to-female aggression, where injuries would be expected to appear frontally. In pens where males displayed high levels of aggression, hens appeared to be extremely fearful as observed in their huddling behavior, alert posture, and frequent alarm calls. Male-to-female aggression also likely contributed to the fearfulness of females. To address the problems observed in broiler breeder males, one must understand the factors producing such behavior and whether it arises from aberrations in aggressive behavior, sexual behavior, or both.

Aggressive Behavior of the Domestic Fowl

It has been well established that male-to-female aggression is rare in domestic fowl and its ancestor, junglefowl (Wood-Gush, 1955, 1958a,b; Kruijt, 1964; Collias et al., 1966; Ylander and Craig, 1980; Rushen 1983/84). Guhl (1949) reported social hierarchies of males and females to be separate, with males dominating females passively. However, some aggression between the sexes occurs when strange individuals are mixed (Craig and Bhagwat, 1974). Furthermore, aggression between hens has been observed to decrease in the presence of a dominant third party, particularly when the dominant individual is male (Craig and Bhagwat, 1974: Ylander and Craig, 1980; Bshary and Lamprecht, 1994). The lower frequency of aggression when the third party is a dominant female suggests that the inhibiting factors are social rather than sexual. Females also tend to avoid males that behave aggressively toward other males (Guhl, 1949; Wood-Gush, 1958a; Rushen, 1983/84), implying that when aroused, males may direct aggression toward females. Rushen (1983/84) suggested that much of the male-to-female aggression he observed was associated with low-status males. Similarly, female-to-male aggression was found to occur in situations where males were of similar size to females (Wood-Gush, 1956). These findings suggest that hierarchies are not separate, but that dominance of the male is rarely contested due to inter-gender differences in physical and physiological attributes.

Because frustration associated with feed deprivation is known to cause chickens to behave aggressively (Duncan, 1970), it came as a surprise that the males with feed provided ad libitum were the most aggressive in the current experiment. The high frequency of crowing by males fed

ad libitum suggests competition between males, either within pens or between neighboring pens from which males could be heard and not seen. Thus, a high frequency of inter-male aggression could be expected. However, the large size of males fed ad libitum should not have predisposed them to problems of maintaining dominance over females, and consequently, one would expect male-to-female aggression to have been low; this was not the case.

Aggression has been shown to increase in response to frustration associated with feed deprivation (Duncan and Wood-Gush, 1971), again raising the expectation that males fed ad libitum would be the least aggressive. Feed-restricted broilers displayed more aggressive pecks during the rearing phase than those fed ad libitum (Mench, 1988; Shea et al., 1990; Mench et al., 1991). Aggression tended to occur at the feeder and was likely associated with frustrated feeding behavior. It is possible that in the current experiment, feed-restricted males were as aggressive as those fed ad libitum, but allocated their time differently. Feed-restricted males may have spent more time searching for food or may have redirected their frustration to stereotypic spot-pecking (Kostal et al., 1992; Savory and Maros, 1993; Hocking et al., 1996). Frequency of pecking at the feeder was not recorded. Also, observations were not taken during feeding time, and it is possible that the aggression of feed-restricted birds observed in other experiments was specific to feeding behavior.

Although all strains behaved more aggressively when feed was provided ad libitum, large genetic differences in aggressiveness of males were observed. Aggression was much greater in the broiler breeder strains than in the commercial laying strain observed (independent of the feeding regimen), but was not found to differ between the broiler breeder strains observed. Craig and Muir (1998) caution against drawing conclusions regarding breed differences when observing a limited number of strains, because large differences in behavior have been observed in selected lines within breeds. For example, White Leghorn strains differ markedly in the occurrence of agonistic behavior (Al-Rawi et al., 1976) and feather-pecking (Craig and Lee, 1990).

Selection for divergent strains has established that there is a genetic component to aggression (Siegel, 1959; Guhl et al., 1960; Bhagwat and Craig, 1978). However, aggression in many of these experiments involved paired contests in which winners were deemed more aggressive, confounding aggressiveness with social dominance. Selection for aggressive motivation has long been practiced in the breeding of fighting game-cocks, in which strains display characteristic fighting patterns and intense aggressive motivation (Atkinson, 1977). Guhl et al. (1960) suggested that aggressiveness in game-cocks is manifested in reduced submissiveness relative to junglefowl, which display high levels of both aggression and submission. It is interesting that broiler breeders scored higher for aggression in all categories measured, because different methods of scoring aggressiveness are often not correlated (Archer, 1988). It is possible that during selection of superior males, or as a result of genetic drift within inbred lines, broiler breeder males have become generally more aggressive.

Sexual Behavior of the Domestic Fowl

Aggression and social hierarchy formation develop at an earlier stage than sexual behavior in domestic fowl. In a study of junglefowl, Kruijt (1964) described sexual aggression as a typical developmental stage of mating behavior. Aggressive elements remained in the copulatory sequence until males became sexually experienced, after which sexual aggression was rare. Wood-Gush (1958a,b) also noted aggressive elements in the early mating behavior of Brown Leghorn cockerels, which decreased as males became sexually experienced. Immaturity cannot account for the sexual aggression of broiler breeder males observed in the current experiment, because observations were taken 5 wk following mixing with females, and neither behavior nor fertility were found to be affected by week and hence, age. It would also be expected that feed-restricted broiler breeders would be the most sexually aggressive, because feed restriction delays sexual maturity (North and Bell, 1990). However, it is possible that broiler breeder strain males are, in fact, developmentally retarded and have become halted at an early stage of sexual development.

Correlations of androgen metabolism and the hypothalamic region of the brain suggest that links between aggressive and copulatory motivation are likely (Harding, 1983, 1986). It has been hypothesized that courtship displays arise from conflicting attack, escape, and copulatory motivations in the interactions of males with females (Wood-Gush, 1954, 1956, 1958a,b; Kruijt, 1964; Bastock, 1967; Feekes, 1971). Displays may function as mechanisms of de-arousal in situations of conflict. Displays are also likely important in signalling intent during social interactions and in maintaining social cohesion.

In the current experiment, frequency of copulation and mounting did not differ as a result of feeding regimen, which suggests that sexual motivation of males was unaffected. Waltzing was performed twice as frequently by males fed ad libitum. Wood-Gush (1956) suggested waltzing to be displayed when aggressive motivation is high relative to motivation for copulation or escape. Because waltzing was the only element of sexual behavior to be affected by feeding regimen, it may be concluded that waltzing reflected a stronger aggressive motivation than sexual motivation. This hypothesis is supported by the greater aggressive behavior displayed by males fed ad libitum (see above). It was surprising that frequency of tidbitting was unaffected by feed restriction. Feekes (1971) found ground-pecking, displayed by male junglefowl during aggressive interactions, to be influenced by factors controlling feeding. Males that were hungry ground-pecked more frequently when confronted by a rival male. Ground-pecking occurring in tidbitting displays likely results from different motivating factors than in male-to-male aggressive situations. Also, feed-re-

stricted males displayed at lower frequencies in general, and it is possible that the level of hunger experienced decreased motivation for social interactions in favor of foraging.

Frequency of copulation was not found to differ between the genetic strains observed. However, there were large differences in the performance of the full sexual behavior repertoire. Courtship displays were performed significantly less frequently by broiler breeder strains, with the exception of the aggressive waltzing display. Thus, broiler breeder males were motivated to copulate, but were not communicating with the females. Deficiencies in courtship displays, particularly in tidbitting, which attracts females to the male, likely accounted for the high frequency of forced copulations and unsuccessful mating attempts of broiler breeder males. The large size of broiler breeder males likely contributed to difficulty in mating (Duncan et al., 1990). However, the fact that broiler breeder males were able to mate when females adopted a sexual crouch indicates that willingness of the female was a more important factor. Furthermore, if physical limitation contributed to the behavior of broiler breeder males, it would be expected that differences would be exacerbated in males fed ad libitum. To the contrary, fertility did not differ between feed-restricted males and those fed ad libitum, regardless of genetic strain. Fertility was also unaffected by week and hence, age for the first half of the breeding season. Similarly, if the large size of broiler breeder males limited their ability to perform courtship displays, one would expect differences resulting from feeding regimen and age. Although waltzing was performed more frequently by males fed ad libitum, displays of high step advance and tidbitting did not differ as a result of feeding regimen. None of the courtship displays were found to differ with week and hence, age. Because this experiment terminated when the flock was 37 wk of age, it is possible that physical limitations would have affected sexual behavior of the males at an older age. However, results from this study indicate that inherent differences in sexual behavior are established at an early age, independent of effects of physical limitations.

Courtship displays are affected by experience, and males may be conditioned to perform particular displays to gain access to females (Kruijt, 1964). It is possible that females learned to avoid broiler breeder males and failed to respond to courtship displays from them. If this were the case, it would be expected that courtship displays would decrease over time; this did not occur. Females also responded positively to displays of laying strain males throughout the experiment. However, it is possible that females learned to avoid broiler breeder males in the 5 wk prior to behavioral observations. Assuming that courtship displays arise from conflicting aggressive and sexual motivation, broiler breeders would be expected to display more frequently than laying strain males, due to the high levels of general aggressiveness in broiler breeder males discussed previously. It is possible that broiler breeder males have low levels of sexual motivation, sufficient to facilitate copulation but not the full repertoire of sexual behavior.

There may be elements in the behavior of females that trigger sexually aggressive responses in males. McBride et al. (1969) studied feral domestic fowl on an uninhabited island off the coast of Queensland, Australia. They noted that forced copulations occurred when females ran or flew down from roosting areas in trees, apparently stimulating males to chase. Casual observations in commercial conditions indicate that females remain on raised slatted areas of the barn when broiler breeder males are particularly aggressive. It is when females jump down from the slats that attacks by males often occur. Arousal, resulting from surprise in such circumstances, could give rise to aggressive responses by males that could cross over into sexual motivation when closer proximity to the hen occurs. However, behavior of females can explain neither the sporadic occurrence of male aggression in commercial conditions, nor the difference in sexual aggressiveness of broiler breeder and laying strain males in identical conditions. The motivation of broiler breeder strain males to react aggressively must be greater than that of laying strain males.

In summary, the problems associated with aggressiveness in broiler breeder males are not a result of frustration associated with feed restriction. There are genetic factors that produce differences in both general aggressiveness and sexual aggressiveness in male domestic fowl. The mechanisms producing sexual aggressiveness involve elements of social cognition, such as deficiencies in courtship behavior. Further research would be beneficial to determine whether behavioral changes result from genetic drift from the foundation stock or from correlated physiological changes of meat production.

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