Genotype-by-Environment Interaction with Broiler Genotypes Differing in Growth Rate. 3. Growth Rate and Water Consumption of Broiler Progeny from Weight-Selected Versus Nonselected Parents under Normal and High Ambient Temperatures

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ABSTRACT One cycle of high-intensity selection on BW was conducted to study correlated effects on performance under high ambient temperature (AT). From a large flock of a commercial sire-line, 3 males and 15 females with the highest BW at 35 d of age were mated and produced a group of 120 BW-selected chicks. Three average-BW males and 15 average-BW females from the same flock were mated to produce a control group of 120 chicks. On Day 17, the two groups were equally divided between two temperature-controlled chambers and housed in individual cages. One chamber was set to a normal AT (NAT; constant 22 C) and the second chamber to high AT (HAT; constant 32 C).

Under NAT, the relative advantage of the selected broilers over the controls did not change from 17 to 42 d of age, averaging about 15% for BW gain and 9.7% for feed consumption. These differences were halved under HAT from Days 17 to 28 and were reversed from 28 to 42 d of age, when the selected broilers consumed significantly less feed and gained less BW than the controls. Water-to-feed ratio was measured in each AT treatment. From 28 to 42 d of age, averaged over the two groups, birds under HAT consumed 2.5 g water/g of feed compared to only 1.5 g water/g feed under NAT.

The diminished superiority of the selected broilers under HAT led to a substantial genotype-by-environment interaction involving high AT and within-stock genetic differences in growth rate. It appears that broilers selected for rapid growth under optimal conditions do not achieve their genetic potential under high AT. Thus, specific indicators of adaptation to heat, possibly water consumption or body temperature, should be added to commercial selection for rapid growth to improve broiler performance in hot climates.

(Key words: selection, ambient temperature, water consumption, body temperature, weight gain)

INTRODUCTION

Tremendous genetic progress has been observed for broiler growth over the last few decades (Havenstein et al., 1994a,b; McKay et al., 2000). However, this dramatic increase in growth rate (GR) and the reduction in time needed to achieve market weight under optimal conditions have not been accompanied by similar improvements under suboptimal conditions. High ambient temperature (HAT) has been a major factor hindering production of poultry meat in hot climates, especially in developing countries where farmers cannot afford costly artificial control of ambient temperature (AT) in broiler houses. Growth rate and meat yield of contemporary commercial broilers is substantially depressed by the environmental stress caused by HAT (Howlider and Rose, 1987, 1989; Geraert et al., 1996; Deeb and Cahaner, 2001a). These negative effects have been more pronounced in chicken genotypes (breeds or lines) with higher BW and more rapid GR than in those with lower BW and GR (Adams and Rogler, 1968; Washburn et al., 1992; Eberhart and Washburn, 1993; Yunis and Cahaner, 1999; Emmans and Kyriazakis, 2000). All of these cases are genotype-by-environment interaction, in which genotypes are lines or breeds differing in their GR, and the environments are normal vs. HAT (Cahaner et al., 1999). Although these conclusions appear to be accurate, they might be confounded with other differences in the overall genetic background between breeds or differently selected lines (Deeb and Cahaner, 2001a). Even broiler stocks that exhibited

Abbreviation Key: AT = ambient temperature; BT = body temperature; FC = feed consumption; FE = feed efficiency (WG/FC); GR = growth rate; HAT = high AT treatment (constant 32 C); NAT = normal AT treatment (constant 22 C); WC = water consumption; WG = BW gain; W:F = WC to FC ratio; W:G = WC to WG ratio.
similar GR under standard commercial management in a temperate climate differed in the magnitude of heat-induced reduction in GR under a hot climate, leading to a significant stock-by-season interaction (Yalcin et al., 1997). On the other hand, in a comparison between dwarf and normal-sized broilers from segregating families, which therefore had similar genetic backgrounds and differed only in GR and BW, no advantage was found for the small body size (dwarf) broilers under HAT (Deeb and Cahaner, 2001b). These results suggest that commercial broiler stocks differ in their response to HAT, possibly due to differences in their overall genetic background.

Improving GR under HAT can be achieved by better understanding the limiting factors inhibiting broiler growth under these stress conditions. Water consumption (WC) per unit of feed consumption (FC) or BW gain (WG) increases with AT. It appears that the importance of sufficient WC in hot climates is higher for broilers with higher GR. Marks (1980, 1985) reported higher water-to-feed ratios in lines selected for rapid growth than in nonselected lines. Group-based WC under medium AT constant and cyclic regimes were evaluated in two recent studies (May et al., 1997, 2000), but there are no reports on the relationship between individual WC, HAT, and GR in populations of modern, fast-growing broilers. The aim of this study was to conduct one cycle of high-intensity selection for high BW, thus generating BW-selected and control groups of broilers sharing the same genetic background, and to compare these groups for their GR, FC, and WC under normal vs. high AT.

**MATERIALS AND METHODS**

**Stock, Temperature, and Husbandry**

Three males and 15 females were selected from the birds with highest BW (within sex) at 35 d of age in a large flock (n ≅ 10,000) of a commercial sire-line stock. An additional three males and 15 females were selected from the same flock with BW close to the flock average. Each male was mated with five similarly selected females, producing about 40 progeny in a single hatch. The group of 120 progeny of the BW-selected parents was designated as “selected,” whereas the group produced by the average-BW parents served as a control. All 240 1-d-old chicks were vent-sexed, wing-banded, and reared together on a litter of wood shavings. Brooding AT was set at 35 C on Day 1 and was reduced by 2 C every 3 d. At 17 d of age, chicks from each group were divided into two temperature-controlled chambers, equally representing the two sexes and the families within group. In these chambers, chicks were assigned at random to individual cages, each equipped with its own feed trough and a drinking cup connected to a separate water container. One chamber was set to normal AT (NAT), starting at 25 C on Day 17, decreasing to 22 C on Day 21, and maintained constant at that level up to Day 42. The second chamber was set to HAT, starting at 25 C on Day 17, gradually increasing to 32 C on Day 21, and maintained constant at that level up to Day 42.

A standard feeding program with commercial diets ad libitum was used (21 and 18% CP, 3,200 and 3,300 cal/g ME during the brooding period and in the cages, respectively). Continuous light and unlimited water were provided throughout the experiment.

**Measurements**

Each chick was weighed at 3, 14, 17, 21, 28, 35, and 42 d of age (when the experiment was terminated). Individual feed intake was measured from 17 to 42 d of age, and average daily WG, FC, and feed efficiency (FE = WG/FC) were calculated for each of the four age intervals (17 to 21 d, 21 to 28 d, 28 to 35 d, and 35 to 42 d). Individual WC was measured from 17 to 42 d of age for 160 birds, equally representing the two AT treatments, the selected and control groups, and sex. For these birds, WC, WC-to-FC ratio (W:F), and WC-to-WG ratio (W:G) were calculated for the same four age intervals. Rectal temperature, an expression of body temperature (BT), was measured by digital thermometer (± 0.1 C) with a 7-cm insertion probe (Sika TT 7070) and recorded when the reading was stable for 15 s. Each bird was represented by the mean of three BT measurements, 12 h apart, during the last 2 d of the experiment (41 to 42 d of age).

**Statistical Analysis**

Least-square means of six BW measurements and four growth intervals were used to draw Figures 1 to 3. For tabular presentation and statistical analyses, growth and consumption data were calculated for two growing periods: from 17 to 28 d of age and from 28 to 42 d of age. The data from each measurement and growing period were subjected to a three-way ANOVA with the genetic group (G), AT, and sex (S) as main effects and all their interactions, according to the following model:

\[ y = \mu + G + AT + S + GxAT + GxS + ATxS + GxATxS + e \]

where Y is the dependent variable, \( \mu \) is the grand mean, and e is the random error term. Tukey’s honestly significant difference test was used for multiple comparisons among least-square means of group and AT combinations. All statistical analyses were carried out with JMP® software (SAS Institute, 2000).

**RESULTS**

Detailed results from all measurements and age intervals are illustrated in Figure 1 (BW), Figure 2 (WG, FC, and FE), and Figure 3 (WC, W:F, and W:G). To simplify the statistical analyses and the interpretation of the results, growth and consumption data were calculated for
two growing periods, 17 to 28 d and 28 to 42 d of age, and analyses were conducted for each period separately. As expected, the sex effect was highly significant but neither of the interactions of genetic group × sex or genetic group × AT × sex was significant; hence means over sexes are presented for each combination of genetic group and AT treatment. Significant interactions of genetic group AT and AT × sex were found for several traits; they are described and discussed in the text.

**BW, WG, FC, FE, and BT**

In response to selection of the parents, the selected group had higher BW than the control group at all ages and under both AT treatments (Figure 1; Table 1). Under NAT, the advantage of the selected group over the control group in BW and FC remained quite constant from 17 to 42 d of age (about 15 and 10%, respectively), hence the difference between the groups in BW increased from about 10% at 17 d of age to 13.5% (2,386 vs. 2,103 g) at 42 d of age (Figures 1 and 2; Table 1). Relative to NAT, the HAT treatment considerably reduced BW, WG, FC, and FE in both groups (Figures 1 and 2). With the combined data for 17 to 28 d of age, the effect of AT on BW, WG, and FC was highly significant, but the deviation between the selected and control groups was only significantly lower at HAT vs. NAT for WG, leading to a highly significant interaction of genetic group × AT (Table 1).

During the last 2 wk (28 to 42 d of age), WG and FC of both groups were further reduced by HAT. However, this highly significant effect was more pronounced in the selected group than in the control, and, consequently, under HAT the difference in BW between the selected and control groups declined with age to only 46 g (3.3%) at 42 d of age, leading to a highly significant interaction of genetic group × AT (Table 1). From 28 to 42 d of age, WG and FC under HAT of the selected broilers were significantly lower (by −12.8 and −9.8%, respectively, Table 1) than those of the control broilers, whereas under NAT the selected broilers maintained a highly significant advantage of 15.2 and 10.3% in WG and FC, respectively. These differences in response of the selected and control broilers to AT resulted in highly significant interactions of genetic group × AT.

For WG and FC in the 28-to-42-d period and for BW at 42 d of age, the interaction between AT and sex was also highly significant (Table 1). As expected under NAT, males (averaged over both groups) exhibited higher WG and FC than females (79 vs. 66 g/d in WG and 170 vs. 150 g/d in FC, respectively), whereas under HAT, males and females exhibited similar mean WG (25 g/d) and FC (88 g/d) during the last 2 wk. The FE of both groups was also significantly reduced by HAT, as early as Days 17 to 28, and to a larger extent during the 28-to-42-d period (Figure 2c; Table 1). The broilers from the two groups exhibited similar mean FE under both AT treatments, because under NAT FE was measured at the same age and not the same BW.

The average of three BT measurements during the last 2 d (Days 41 and 42) was calculated for each bird. The HAT treatment increased BT significantly, by about 1.2 C in both groups, whereas group means within AT treatments were almost identical to each other (Table 1).

**WC**

Between 17 and 28 d of age, WC (g/d per bird) was significantly affected by group, AT, and sex (Table 2). At
both age intervals (17 to 21 and 21 to 28, Figure 3a), higher WC was exhibited by the selected broilers than by their control counterparts, by broilers under HAT vs. those under NAT (Figure 3a), and by males compared to females (data not shown). The selected broilers consumed about 9.3 and 5.3% more water than their control counterparts under NAT and HAT, respectively, and within each genetic group, HAT increased WC during 17 to 28 d by about 26%, 217 vs. 176 g/d and 206 vs. 161 g/d in the selected and control groups, respectively (Table 2). Under
NAT, the broilers consumed about 1.6 g water/g of feed, whereas under HAT, the W:F was about 50% higher (2.33 in both groups, Table 2). In each AT treatment, mean W:F from 17 to 28 d was very similar in the selected and control groups (Table 2; Figure 3b), because the differences between groups in WC (Figure 3a and Table 2) were similar to those in FC (Figure 2b and Table 1).

The W:G ratio (WC/WG) was also calculated and analyzed. As with W:F, means of W:G from 17 to 21 d of age and 21 to 28 d of age were similar in the selected and control groups within each AT treatment (Figure 3c). Averaged over the two groups, the broilers under NAT consumed about 2.7 g of water/g of BW gain during the 17-to-28-d period. Under HAT, mean W:G was about 3.5 in
TABLE 1. Means (males + females) of BW, weight gain (WG), feed consumption (FC), feed efficiency (FE = WG/FC), and body temperature (BT) of BW-selected and control broiler groups reared under NAT\(^1\) or HAT\(^2\) and the significance levels derived from three-way ANOVA

<table>
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<tr>
<th>Variable</th>
<th>Age (d)</th>
<th>NAT(^1)</th>
<th>HAT(^2)</th>
<th>Deviation(^3) (%)</th>
<th>ANOVA [P(F)]</th>
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<tr>
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<td>Selected</td>
<td>Control</td>
<td>Selected</td>
<td>Control</td>
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<td>519(^b)</td>
<td>575(^a)</td>
<td>517(^b)</td>
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<td>1,127(^b)</td>
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<td>2,103(^b)</td>
<td>1,452(^c)</td>
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<td>58.7(^b)</td>
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*Means within row lacking common superscript differ significantly [P(F) < 0.05].
\(^1\)NAT = normal ambient temperature; 25 C on Day 17, gradually reduced to a constant 22 C on Day 21 and thereafter.
\(^2\)HAT = high ambient temperature; 25 C on Day 17, gradually increased to a constant 32 C on Day 21 and thereafter.
\(^3\)\(100 \times (\text{selected} - \text{control})/\text{control}\).
\(^4\)NS = not significant; P(F) > 0.05.

TABLE 2. Means (males + females) of water consumption (WC), water-to-feed ratio (W:F), and water-to-BW gain ratio (W:G) of the BW-selected and control broiler groups reared under NAT\(^1\) or HAT\(^2\) and the significance levels derived from three-way ANOVA

<table>
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<th>Variable</th>
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</thead>
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<td>Selected</td>
<td>Control</td>
<td>Selected</td>
<td>Control</td>
<td></td>
</tr>
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<td>161(^d)</td>
<td>217(^a)</td>
<td>206(^b)</td>
</tr>
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<td>3.58(^b)</td>
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<td>3.34(^b)</td>
<td>1025(^a)</td>
<td>9.50(^b)</td>
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</table>

*Means within row lacking common superscript differ significantly [P(F) < 0.05].
\(^1\)NAT = normal ambient temperature; 25 C on Day 17, gradually reduced to a constant 22 C on Day 21 and thereafter.
\(^2\)HAT = high ambient temperature; 25 C on Day 17, gradually increased to a constant 32 C on Day 21 and thereafter.
\(^3\)\(100 \times (\text{selected} - \text{control})/\text{control}\).
\(^4\)NS = not significant; P(F) > 0.05.
the 17-to-21-d interval, and it increased to around 5 in the 21-to-28-d interval, with an average of 4.4 g of water/g of BW gain between 17 and 28 d of age (Figure 3c, Table 2).

Between 28 and 42 d of age, WC was affected by a highly significant genetic group × AT interaction (Table 2). Under NAT, WC continued to increase in both groups but at a higher rate in the fast-growing broilers than in the controls (Figure 3a). Combined over the 28-to-42-d period, the selected group consumed 16.8% more water than the control group (257 vs. 220 g/d, Table 2). Under HAT, WC of the selected broilers was lower from 28 to 35 d than during the previous interval and decreased further in the last week. The WC of the control broilers was higher than that of the selected ones for both intervals (Figure 3a). Averaged over 28 to 42 d, WC of the selected broilers under HAT was lower (−8.6%) than their control counterparts (Table 2). The AT × sex interaction was significant for WC; it was similar to the genetic group × AT interaction, with males behaving like the selected group (mean WC of 258 and 217 g/d under NAT and HAT, respectively), and females behaving like the control group (about 220 g/d under both AT treatments).

Mean W:F increased with AT, from about 1.5 g water/g of feed under NAT to about 2.5 g/g (67% higher) under HAT (Figure 3b, Table 2). For each AT treatment, mean W:F was very similar in the selected and control groups, because the differences between groups in WC (Figure 3a and Table 2) were similar to those in FC (Figure 2b and Table 1). Mean W:G under NAT was also very similar in both groups; it increased to about 3 g/g from 28 to 35 d, then to about 4 g/g from 35 to 42 d, and the two groups averaged 3.36 g/g from 28 to 42 d (Figure 3c, Table 2). Under HAT, W:G increased dramatically with age to about 8 and 11 g/g from 28 to 35 d and 35 to 42 d of age. Averaged for the 28-to-42-d period, mean W:G were 10.25 and 9.5 g water/g of BW gain in the selected and control groups, respectively, but this difference was not significant (Figure 3c, Table 2).

**DISCUSSION**

**Experimental Population Design**

Several studies have demonstrated that growth depression under HAT is more pronounced in fast-growing chicken lines than in slow-growing lines (Washburn et al., 1992; Eberhart and Washburn, 1993; Yunis and Cahaner, 1999; Deeb and Cahaner, 2001a). In the latter study, however, it was suggested that these reported differences in response to heat could result from unknown genetic differences between stocks and not necessarily from the difference in their potential GR and BW. This aspect was addressed by the experimental design of the present study, which did not consist of a comparison between lines that also differed in their overall genetic background. Rather, the two genetic groups compared in the present study were derived from the same population, and hence shared an identical genetic background and differed only in those genes that affect the continuous genetic variation in BW in commercial broiler stocks. After one cycle of intense selection, average BW at 42 d of age under normal conditions (NAT) was 283 g higher in the selected group than the control (2,386 vs. 2,103 g, males + females). Thus, the two groups compared in this study diverged by a magnitude four to five times more than the yearly genetic increase in BW of commercial broilers (McKay et al., 2000).

The large divergence enabled a more sensitive and reliable detection of genotype-by-environment interaction, in contrast to the gradual changes occurring in commercial broilers from year to year. In most previous studies, to achieve large divergence in BW, the slow-growing group was a stock not selected for GR and was compared to contemporary commercial broilers. Therefore, the conclusions drawn from those studies must have limited relevance to future broiler breeding and husbandry. In the present study, contemporary broilers were used as the slow-growing group, and genotypes representing future broilers were taken as the fast-growing group. Moreover, because this large divergence in BW was achieved by a single cycle of selection, inbreeding and a potential confounding effect due to genetic drift were avoided, leaving the two groups with identical genetic backgrounds.

**Performance Under NAT**

Under NAT, as expected, WG of each group was quite constant from 21 to 42 d of age, averaging about 75 and 65 g/d in the selected and control groups, respectively (Figure 2a). The divergence between the groups in FC under NAT increased with age, from about 10 g/d (Days 17 to 28) to 20 g/d during the last week, reflecting the increasing difference in BW (Figure 2b). The higher growth rate of the selected group was due to increased FC, whereas FE was similar in both groups at all age intervals. However, the control broilers would have to consume about 5 d worth of additional feed to reach a mean 42-d BW of the selected group.

**Effect of HAT on Performance**

From 17 to 21 d of age, AT in the HAT chamber was elevated gradually from 25 to 32 C and held constant thereafter. During the following week (Days 21 to 28), WG hardly changed and was identical in both groups (Figure 2a). Mean FC of chicks from both groups increased during this week but to a lower level than FC of their counterparts under NAT (Figure 2b). Similar results were obtained by Deeb and Cahaner (2001a); during the gradual elevation from normal AT to high AT, FC of broilers did not change, but their WG was lower than expected. These results indicate that during the acclimatization period, WG stabilized but FC continued to increase, probably because a larger proportion of the consumed energy is used for thermoregulation.
As expected, performance traits were reduced by HAT, compared to NAT, but this effect was more pronounced in the selected group. As a result, the genetic advantage of the selected group in WG and FC was not materialized under HAT, in which both groups exhibited similar WG and FC. Actually, the broilers with higher potential exhibited lower mean FC and WG after 4 wk of age, in agreement with the results reported by Settar et al. (1999), in which sire families represented different levels of genetic potential, expressed in actual growth during the temperate spring season. Family differences in WG from 4 to 7 wk of age disappeared, and even slightly reversed, when the same families were reared under hot summer conditions.

The interaction between the genetic groups and AT treatments was most evident for feed intake from Days 28 to 42, in which under HAT mean FC of the selected group was significantly lower than that of the control group. Mean BT was significantly higher under HAT than under NAT, in agreement with previous studies (Deeb and Cahaner, 1999, 2001b) but with no difference between the groups. When BT was measured on Days 41 and 42, the selected broilers under HAT averaged lower FC than their control counterparts. The broilers reared under NAT were within the thermoneutral zone; hence, despite the differences in FC and WG between the selected and control groups, both had similar mean BT. In contrast, broilers under HAT have difficulty dissipating the internally produced heat, which is positively correlated with feed intake and metabolism (Deeb and Cahaner, 1999). Based on theoretical considerations, it was suggested that as broilers are selected to grow faster, they tend to generate more heat and, hence, need lower AT to maintain their BT and to materialize their genetic potential for rapid growth (Emmans and Kyriazakis, 2000). The results of the present study empirically confirm this suggestion; broilers with higher genetic potential for rapid growth under optimal conditions, when exposed to high AT, apparently had to lower internal heat production by reducing their feed intake to maintain the same BT as their control counterparts who were able to consume more feed under these conditions.

For FC and WG from 28 to 42 d, there was also a significant interaction of sex × AT. The nature of this interaction was very similar to the genotype × AT interaction. Under NAT, males exhibited their normal advantage over females, whereas under HAT, males and females had similar mean WG and FC during the last 2 wk. Higher sensitivity of males compared to females under high AT is well documented (e.g., Howlider and Rose, 1987), and an interaction between AT and sex has been reported by Cahaner and Leenstra (1992). In that study, females were heavier than males at 8 wk of age when reared at a constant 32 C and fed a high-protein diet, which enhanced the effects of high temperature (Cahaner et al., 1995). The similar response to HAT of broilers with higher potential for rapid growth, either due to selection or to sexual dimorphism, indicates the general physiological nature of this phenomenon, namely lower heat tolerance, is clearly associated with higher potential for rapid growth under optimal conditions.

**WC**

In agreement with previous reports (Pesti et al., 1985; Xin et al., 1994; Alleman and Leclercq, 1997), WC under NAT increased linearly with age, with the difference between the selected and control groups reflecting their difference in FC. The strong association between WC and FC was evident from the W:F, which remained quite constant from 21 to 42 d of age and was very similar in both groups (Figure 2b). As higher AT increased evaporative water loss (Bailey, 1990), WC in both groups was higher under HAT than that of their counterparts under NAT but only up to 28 d of age. During the following 2 wk, WC was reduced, reflecting the HAT-induced reduction in FC. Alleman and Leclercq (1997) reported that at 32 C (similar to HAT), WC did not change with age, whereas under constant 22 C (similar to NAT), WC increased with age, and at 35 d of age it exceeded WC under 32 C. Also under HAT, W:F was similar in both groups and increased only slightly with age.

In a recent study, May et al. (2000) also found that under low air velocity and constant AT, WC and FC do not change much with age. However, that study and the present one differ in type of waterers (nipple vs. cups, respectively), and as nipples have been found to inhibit WC under HAT (May et al., 1997), these studies should be compared with caution. It was obvious, however, that under HAT, W:F was almost twice as large as compared to NAT, indicating a higher demand for water under HAT. Similar results were reported by Alleman and Leclercq (1997), with W:F = 1.9 under constant 22 C and W:F = 3.1 under constant 32 C. Temperate vs. hot climates have also been found to affect the W:F ratio, changing it from 1.6 to 1.9, respectively (Pesti et al., 1985). In the present study, the two groups exhibited similar means of drinking-related traits, except for WC during the last 2 wk (Days 28 to 42), in which a significant genotype × AT interaction was found, similar to that of FC during the same period with the selected broilers under HAT consuming less water than their control counterparts. This difference could reflect the comparable difference in FC, which has been suggested to be related to different thermoregulation efficiencies. It is possible, however, that the selected broilers under HAT, for unknown reasons, could not consume as much water as their control counterparts, and this decreased WC, in turn, reduced their FC and WG.

The results of the present study clearly demonstrate that rapid GR alone is responsible for the increasing sensitivity of broilers to HAT. Therefore, the increase in genetic potential of commercial broilers for faster growth under optimal conditions cannot be materialized under HAT conditions. Moreover, the results suggest that future broilers with genetically higher potential for rapid growth may exhibit lower performance under HAT, as compared to past or current broilers. Therefore, specialized breeding
programs, using genetic information on traits that reflect adaptation to heat, such as WC or BT, must be devised to counteract this expected change. However, more detailed genetic research is needed, using a family-structured population of contemporary breeding stock, to devise such breeding programs and assess their direct and indirect effects on broiler performance under a wide range of optimal and suboptimal conditions.

REFERENCES


