GENETICS

Divergent selection for muscle color in broilers

I. D. Harford,* H. O. Pavlidis,† and N. B. Anthony‡

*Heritage Breeders, Princess Anne, MD 21853; †Cobb-Vantress, Siloam Springs, AR 72761; and ‡Department of Poultry Science, University of Arkansas, Fayetteville 72701

ABSTRACT One consumer-related physiological abnormality that is a recent concern for the poultry industry is atypical meat quality. Currently in the processing plant, meat is characterized on appearance such as tears, bruises, discoloration, or missing parts. Unfortunately, this method ignores physical properties such as palatability, texture, tenderness, taste, color, pH, and water-holding capacity (WHC). The growing demand for a convenient, economical, and palatable product has shifted the market toward value-added poultry products. The effect of a meat’s physical properties on its marketability and versatility has become apparent to processors attempting to utilize poor quality meat. After 8 generations of divergent selection for muscle color or lightness (L*) in broilers, muscle quality parameters were investigated. The two broiler lines divergently selected for high (HMC) and low (LMC) muscle color along with their randombred control line (RBC) were included in the study. Heritability estimates for L* were 0.47 ± 0.05 and 0.51 ± 0.05 in the HMC and LMC lines, respectively. For generation 8, the mean L* for the HMC, RBC, and LMC lines were 53.91, 49.70, and 46.86, respectively. Selection for increased L* was found to result in increased breast fillet yellowness (b*), whereas selection for decreased L* resulted in an increase in breast fillet redness (a*). Selection for increased L* has resulted in increased rate of pH decline over time, whereas selection for decreased L* has resulted in a decreased rate of pH decline. The HMC line exhibited a higher percentage fillet drip loss than both the LMC and RBC lines, which did not differ from each other. Overall selection for L* was effective in modifying breast muscle color as well as correlated responses associated with atypical poultry meat such as drip loss and postmortem muscle pH. These selected lines can serve as resource populations for the study of PSE and DFD-like meat in poultry and demonstrate that L* selection could be applied to primary breeding programs as a way to improve or manage muscle quality in pedigree elite lines.

Key words: pale, soft, and exudative meat, dark, firm, and dry meat, muscle quality, genetic selection, L*

INTRODUCTION

Intense selection for growth, feed conversion, and white meat yield by primary breeders has led to tremendous gains in the commercial performance of broilers. It has been reported that 85 to 90% of the differences between today’s bird and the average bird of 60 yr ago is due to genetic selection (Havenstein et al., 1994a,b, 2003a,b). Unfortunately, the advancements in these commercially important traits have resulted in unintended consequences such as increased skeletal abnormalities (Julian, 1998; Cook, 2000), increased carcass fat (Soller and Eitan, 1984; Chambers, 1990), decreased reproductive performance (Siegel and Dunnington, 1985; Qureshi and Havenstein, 1994), increased ascites (Julian, 2000), and increased atypical poultry meat (Barbut, 1997a,b, 1998; Anthony, 1998).

Atypical poultry meat can be broken down into 2 classes: pale, soft, and exudative (PSE)-like or dark, firm, and dry (DFD)-like. The attention on atypical poultry meat has increased greatly as the industry has shifted from whole birds to further processed and ready-to-eat products. The production of atypical meat has been difficult to quantify because factors such as breed (Gardzielewksa et al., 1995; McCurdy et al., 1996; Musa et al., 2006), rearing environment (Sayre et al., 1963; Owens and Sams, 2000), processing plant (de Femery and Pool, 1960; Owens and Sams, 2000), chilling method (Offer, 1991; McKee and Sams, 1998; Alvarado and Sams, 2002, 2004), nutrition (Cheah et al., 1995; Ferket et al., 1995; Olivo et al., 2001), and stunning method (Gregory, 2007) have been reported to affect its incidence. In broilers the incidence of PSE-like fillets has been reported to range in processing plants anywhere from 0 to 47% (Woelfel et al., 2002), and in...
turbkeys that incidence ranges from 5 to 40% (Barbut, 1996). Economic losses in atypical poultry meat are associated with modified muscle functionality. In PSE-like meat, the economic losses are associated with reduced water holding capacity (WHC), increased cook loss, decreased tenderness, and decreased emulsification capacity (Allen et al., 1998; Sosnicki et al., 1998; Qiao et al., 2001). In DFD-like meat, the economic losses are associated with an atypical color and after-flavor, dry and sticky texture, and decreased product shelf-life (Allen et al., 1998; Fletcher, 1999).

The characteristics of PSE-like and DFD-like meat stem from an abnormal rate of postmortem muscle glycogenolysis (Wismer-Pedersen, 1959). Animals with PSE-like meat generally have been stressed moments before slaughter, resulting in increased rate of postmortem pH decline (Owens and Sams, 2000; Qiao et al., 2001). The DFD-like meat is essentially the opposite of PSE-like meat and occurs when an animal has been stressed much earlier before slaughter, resulting in depletion of glycogen reserves and subsequent reduction of postmortem pH decline (Hedrick et al., 1989; Gregory, 1994; Lawrie, 1998; Qiao et al., 2001).

Quantitative characterization of atypical poultry meat can be determined by the objective measurement of its functional properties. The most common characteristics measured to classify atypical meat include muscle color (Barbut, 1993, 1996; McCurdy et al., 1996), muscle pH (Jeacocke, 1977; Dosler et al., 2007), WHC (Wierbicki and Deathrager, 1958; Barbut, 1993; Owens et al., 2000a,b), and cook loss (Owens et al., 2000a,b). Measuring muscle color with the use of a colorimeter is the most widely accepted method for characterizing atypical or normal meat (Barbut, 1993, 1996; McCurdy et al., 1996). The use of L* for meat quality prediction is favored as it is easily measured, allowing for quick and repeatable measurements on a large number of breast fillets. The L* has also been reported to be highly heritable, as well has have a very strong genetic correlation with both muscle pH and WHC (Le Bihan-Duval et al., 2001, 2008; Gaya et al., 2006). The high heritability, strong genetic relationship with muscle pH and WHC, combined with the relatively low cost and ability to measure on a large number of individuals make L* a favorable tool for use in commercial breeding programs as a way to monitor or select for meat quality.

Divergent selection for PSE- and DFD-like poultry meat was accomplished through selection on high and low L*, respectively. This bi-directional selection program allows for the exploration of the genetic relationships and correlated responses that are associated with both PSE- and DFD-like meat in broiler chickens. This selection program may also allow for determination of the underlying genetic mechanisms associated with atypical poultry meat through molecular analysis. The purpose of this research was 2-fold: determine if selection for L* could influence PSE and DFD-like charac-

**MATERIALS AND METHODS**

Birds from a randombred broiler line (RBC) were reared and processed at 56 d of age at the University of Arkansas. Breast fillets were characterized for 24 h postmortem muscle color using a Minolta CR-300 Colorimeter (Minolta Chroma Meter CR-300, Minolta Italia S.p.A., Milano, Italy) as described by Petracci et al. (2004). Based on those results, divergent selection was initiated for muscle color to investigate the effects of selection for muscle color on product quality. However, evaluation of muscle color is currently a terminal measure; therefore, progeny must be tested from each sire to obtain sufficient information to make appropriate selection decisions in these lines. The following methods were developed to address the issues associated with selection for an invasive trait.

**Line Formation**

The base population used for this study is a broiler type RBC currently maintained at the University of Arkansas. Briefly, the RBC population was established by forming a composite of commercial parent stocks available in 1997. The initial cross includes all combinations of 7 male (Avian 89, Ross SP, Hubbard HI-Y, Case, Cobb 500, Peterson Regular, and Shaver) and 6 female (Cobb 500, Ross 508, Arbor Acres Classic, Hubbard HI-Y, Case 573, and Shaver Yield B) strain sources. Second generation matings were designed to match in such a way as to provide only 25% contribution from a founder parent type. In addition, an equal number of progeny was produced from each mating combination. Random matings were practiced from the third generation on except for the avoidance of brother-sister mating. The population size was maintained at 24 sires with 3 dams per sire.

In 2005, divergent selection for muscle color was initiated to create HMC and LMC lines. The methods used for the formation of these lines were consistent with that used for lines selected for ascites incidence (Pavlidis et al., 2007). The lines were designated as HMC and LMC, which represented lines selected for high and low 24 h postmortem L*, respectively. All matings were performed by artificial insemination, and complete pedigree information was collected every generation. Six hatches of RBC chicks were produced to generate the lines. Hatches 1 and 2 were processed to generate the color data necessary for selection, whereas hatches 3 through 6 generated the sibs necessary for line reproduction. Therefore, hatches 1 and 2 were reared to 8 wk of age (generations 1 to 2) and 6 wk of age (generations 3 to 8). When the lines were first established, 8 wk was chosen as the selection age. After evaluating families at 6 and 8 wk of age, it was observed that no interaction

Muscle Quality Parameters

Available birds of the first 2 hatches from the eighth generation of selection were not only measured for L*, but also for fillet drip loss (DL; %) and muscle pH. Each pen was stocked with 24 birds and equal numbers for each sex line combination for the HMC, RBC, and LMC lines. At 6 wk of age feed was removed for 12 h after which batches were created with 3 randomly chosen pens. Birds were then processed in the same way as previously described for sib-data collection.

Data Analysis

Genetic parameter analysis of muscle color traits were conducted in the HMC and LMC line using data from generations 0 to 8. Over the course of 8 generations, 2,986 and 3,509 individuals from the HMC and LMC lines were used for the analysis. Data were analyzed according to DMU procedures outlined by Madsen and Jensen (2000). An animal model was used in both line HMC and LMC for the traits of L*, a*, b*. Single trait runs were conducted for each trait by line to determine the significance of the tested fixed effects as well as to determine if the heritability was different from zero. For all traits, the fixed effect of sex and a combined fixed effect of generation and hatch were found to be significant and used in the model. Phenotypic correlations for muscle color in the HMC and LMC lines for generation 0 to 8 were derived using the Pearson correlation procedure in SAS software (SAS Institute Inc., 1988).

RESULTS AND DISCUSSION

Genetic Parameters for Generations 0 to 8 (L*, a*, b*)

Several researchers have shown that a genetic component exists for muscle color due to flock, breed, and strain variation (Owens et al., 2000b,c; Le Bihan-Duval et al., 2001, 2008; Berri et al., 2005; Gaya et al., 2006; Molette et al., 2006; Musa et al., 2006; Sandercock et al., 2009). However, little work has been done to evaluate the effectiveness of selection for muscle color and its impact on the production of PSE- or DFD-like poultry meat.

Heritability estimates for L* were found to be high for both the HMC and LMC lines at 0.47 and 0.51, respectively (Table 1). These findings are consistent with the results of Le Bihan-Duval et al. (2001, 2008) and Gaya et al. (2006) who reported heritabilities for L* to range from 0.29 to 0.50. Use of the colorimeter to measure L* also yields 2 additional color measures, a* and b*, which are a measurement of redness and yellowness, respectively. Little attention is often paid to these 2 variables with regard to PSE- or DFD-like poul-
try meat because L* is often used as the primary color parameter to classify meat as either PSE- or DFD-like (Smith and Northcutt, 2009). Heritability estimates for a* in the HMC and LMC were found to be moderate, ranging from 0.32 to 0.35 in the HMC and LMC lines, respectively (Table 1). These heritability estimates are consistent with the ranges previously reported for a*, 0.25 to 0.57 (Le Bihan-Duval et al., 2001, 2008; Gaya et al., 2006). The genetic correlation between L* and a* was reported to be −0.48 by Le Bihan-Duval et al. (2001), and it was found to be −0.58 and −0.48 in the HMC and LMC lines, respectively (Table 1). Phenotypic correlations between L* and a* were also found to be negative with a value of −0.35 in the HMC and −0.46 in the LMC line (Table 2).

For b*, a measurement of yellowness, the heritability has been reported to range from 0.16 to 0.55 (Le Bihan-Duval et al., 2001, 2008; Gaya et al., 2006). In this current study, the heritability for b* was 0.34 in the HMC and 0.30 in the LMC line (Table 1). The genetic correlations between L* and b* were reported to be 0.20 by Le Bihan-Duval et al. (2001) and were found to be 0.48 and 0.43 in the HMC and LMC lines, respectively (Table 1). Phenotypic correlations between L* and b* were found to be 0.56 to 0.57 in the HMC and LMC lines respectively (Table 2). No genetic and low negative phenotypic correlations between a* and b* were found (Tables 1 and 2). This was not consistent with what was reported by Le Bihan-Duval et al. (2001) who reported a positive genetic correlation of 0.54. These differences may be due to differences in selection criteria or genetic architecture of the populations evaluated in both studies.

Muscle Quality Comparisons of HMC, RBC, and LMC Lines

Selection for 24 h L* in the upward and downward directions has resulted in divergence of selected population means (Figure 1). Due to constraints, the RBC line was not continuously evaluated for muscle color until the sixth generation. Although population means vary from generation to generation, divergence of means has steadily increased in progressive generations (Figure 2). On average, the LMC and HMC lines diverged 0.79 L* units per generation. Comparison of the HMC and LMC lines to the RBC line from which they were derived showed that in generation 8 the HMC and LMC lines were not only different from each other but also from the RBC line (Table 3). The HMC line had L* that were higher than the RBC and LMC lines by 4.21 and 7.05 units, respectively (Table 3). The LMC line was 2.84 units lower than the RBC (Table 3). The position of the RBC line mean between the HMC and LMC line means in generation 8 suggests that the selected lines progressed in their respective directions of selection. Evaluation for redness showed the LMC line had a* that were greater than both the RBC and HMC lines, whereas the HMC line had a* that were lower than the LMC and RBC lines (Table 3). Comparison of yellowness showed that the HMC line had b* that were greater than both the RBC and HMC lines, whereas the HMC line had b* that were lower than the LMC and RBC lines (Table 3). It appears that selection for L* resulted in correlated changes in a* and b* that corresponded to the respective direction of selection applied for L*.

### Table 1. High (HMC) and low muscle color (LMC) line1 heritabilities, and genetic correlations2 for muscle color3

<table>
<thead>
<tr>
<th>Item</th>
<th>HMC Line</th>
<th>L*</th>
<th>a*</th>
<th>b*</th>
<th>LMC Line</th>
<th>L*</th>
<th>a*</th>
<th>b*</th>
</tr>
</thead>
<tbody>
<tr>
<td>L*</td>
<td></td>
<td>0.47 ± 0.05</td>
<td>−0.58</td>
<td>0.48</td>
<td></td>
<td>0.51 ± 0.05</td>
<td>−0.48</td>
<td>0.43</td>
</tr>
<tr>
<td>a*</td>
<td>0.08</td>
<td>0.32 ± 0.04</td>
<td>−0.10</td>
<td>0.08</td>
<td>0.35 ± 0.04</td>
<td>−0.13</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>b*</td>
<td>0.08</td>
<td>0.12</td>
<td>0.34 ± 0.04</td>
<td>0.08</td>
<td>0.11</td>
<td>0.30 ± 0.04</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1HMC and LMC lines selected for high and low L*, respectively.
2Heritabilities and SE are on the diagonal line, genetic correlations are above the diagonal line, and genetic correlation SE are below the diagonal line.
3Measured at 24 h postmortem. L* = lightness; a* = redness; b* = yellowness.

### Table 2. High (HMC) and low muscle color (LMC) line1 phenotypic correlations2 for 24-h muscle color3

<table>
<thead>
<tr>
<th>Item</th>
<th>HMC</th>
<th>L*</th>
<th>a*</th>
<th>b*</th>
<th>LMC</th>
<th>L*</th>
<th>a*</th>
<th>b*</th>
</tr>
</thead>
<tbody>
<tr>
<td>L*</td>
<td>−0.35</td>
<td>0.56</td>
<td></td>
<td></td>
<td>−0.46</td>
<td>0.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a*</td>
<td>&lt;0.0001</td>
<td>−0.07</td>
<td></td>
<td></td>
<td>&lt;0.0001</td>
<td>−0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b*</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1HMC and LMC lines selected for high and low L*, respectively.
2Phenotypic correlations are above the diagonal line, and P-values are below the diagonal line.
3L* = lightness; a* = redness; b* = yellowness.
The characteristics of PSE- and DFD-like meat stem from an abnormal rate of postmortem muscle glycolysis (Wismer-Pedersen, 1959). Comparison of postmortem pH at 15 min, 4 h, and 24 h for HMC, RBC, and LMC lines has shown that selection for L* has changed the rate of pH decline. At 15 min postmortem, the HMC line is lower in muscle pH than the RBC and LMC lines (Table 3). At both 4 and 24 h postmortem, the LMC line was higher in muscle pH than the RBC and HMC lines, whereas the HMC line was lower in muscle pH than the LMC and RBC lines.

Because decreased WHC is associated with atypical poultry meat, mainly PSE-like meat, DL as measured over a 20-h period was evaluated in generation 8 for the HMC, LMC, and RBC lines and the results are presented in Table 3. The HMC line had higher DL than both the RBC and LMC line. The LMC line was not different than the RBC line for DL. This observed increased DL in the HMC line is consistent with what has been observed with PSE-like meat (Hedrick et al., 1989; Gregory, 1994; Lawrie, 1998; Qiao et al., 2001) and suggests that selection for increased L* may result in fillets that are more PSE-like and show traits associated with PSE-like meat such as increased muscle color and DL. Additional generations of selection for decreased L* may be required before reduced DL is observed in the LMC line.

### Phenotypic Relationship of Muscle Color, pH, and DL (%)

To better understand how selection for L* has changed correlated traits such as a*, b*, muscle pH, and DL, phenotypic correlations were calculated. Initially, correlations were calculated for each line separately, but they only differed slightly. As a result, the phenotypic correlations were derived from the combined data of all 3 lines (Table 4). The observed correlations between L*, a*, and b* for all 3 lines in generation 8 were similar to what was observed in the HMC and LMC lines for generations 0 to 8. The correlation between L* and muscle pH increased over time, it ranged from −0.28 (15 min) to −0.79 (24 h). The correlation between L* and DL was 0.47. The correlation between DL and muscle pH increased over time as well and ranged from −0.18 (15 min) to −0.44 (24 h; Table 4). The observed correlations between muscle color, pH, and DL are consistent with previous studies (Le Bihan-Duval et al., 2001, 2008; Gaya et al., 2006).

### Table 3. Means for muscle color, pH, and drip loss1 for high muscle color (HMC), low muscle color (LMC), and randombred control (RBC) lines as measured after 8 generations of divergent selection for L*2

<table>
<thead>
<tr>
<th>Line</th>
<th>24-h muscle color</th>
<th>Postmortem pH</th>
<th>Drip loss (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L*</td>
<td>a*</td>
<td>b*</td>
</tr>
<tr>
<td>HMC</td>
<td>53.91 ± 0.28a</td>
<td>3.03 ± 0.08c</td>
<td>5.17 ± 0.14a</td>
</tr>
<tr>
<td>RBC</td>
<td>49.70 ± 0.17b</td>
<td>3.94 ± 0.08b</td>
<td>4.35 ± 0.11b</td>
</tr>
<tr>
<td>LMC</td>
<td>46.86 ± 0.20c</td>
<td>4.91 ± 0.09a</td>
<td>3.95 ± 0.13c</td>
</tr>
<tr>
<td>P-value</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

*a–cMeans with no common superscripts are different (P < 0.05).

1Percentage drip loss is defined as [(breast weight at 4 h postmortem − breast weight at 24 h postmortem)/breast weight at 4 h postmortem] × 100.

2L* = lightness; a* = redness; b* = yellowness.
Table 4. Population\(^1\) phenotypic correlations\(^2\) for muscle color, pH, and drip loss\(^3\) for high muscle color (HMC), low muscle color (LMC), and randombred control (RBC) lines as measured after 8 generations of divergent selection for L*\(^4\)

<table>
<thead>
<tr>
<th>Item</th>
<th>24-h muscle color</th>
<th>Postmortem pH</th>
<th>Drip loss (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L*</td>
<td>a*</td>
<td>b*</td>
</tr>
<tr>
<td><strong>Postmortem pH</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 min</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>4 h</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>24 h</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Drip loss (%)</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

\(^1\)Phenotypic correlations were derived from the combined data of the HMC, LMC, and RBC lines.

\(^2\)Phenotypic correlations are above the diagonal line, and \(P\)-values are below the diagonal line.

\(^3\)Percentage drip loss is defined as \[(breast weight at 4 h postmortem − breast weight at 24 h postmortem)/breast weight at 4 h postmortem\] \times 100.

\(^4\)L* = lightness; a* = redness; b* = yellowness.

**General Synthesis**

The heritabilities for L* were found to be high in both the HMC and LMC lines and were consistent with previously reported results (Le Bihan-Duval et al., 2001, 2008; Gaya et al., 2006) suggesting a strong additive component. However, at this point, it is unclear what all possible mechanisms are responsible for muscle color variation (Froning and Hartung, 1967; Froning et al., 1968). Owens et al. (2000a) and Woelfel et al. (2002) found that paler turkey and broiler breasts had lower ultimate pH, cooking yield, and increased DL. Those findings suggest that the pale appearance was due to the PSE condition. In contrast, Berri et al. (2005) found that broilers selected for increased growth rate and breast yield resulted in fillets that had higher pH at both 15 min and 24 h postmortem, and lower iron content, while remaining pale in appearance. Those findings suggest that paleness was caused by mechanisms not associated with the PSE-like condition and is supported by an emerging myopathy of broiler breast meat associated with high yield and growth rate. Conversationally known as wooden or plank breast, it has been characterized as hard, pale, and exhibiting increased muscle pH, exudation, and white striping (Kuttappan et al., 2012, 2013; Sihvo et al., 2013).

Although it is likely there are other mechanisms responsible for muscle color variation that are not associated with the PSE- and DFD-like condition, selection for muscle color appears to have resulted in increased PSE- and DFD-like characteristics in these experimental populations. Selection for increased L* in the HMC line resulted in decreased redness, increased yellowness, increased rate of pH decline, and increased DL of the breast fillet. This increase in DL and rate of pH decline is consistent with PSE-like meat and is one of the economic costs associated with PSE-like meat (Allen et al., 1998; Sosnicki et al., 1998; Qiao et al., 2001). Selection for decreased L* in the LMC line has resulted in increased redness, decreased yellowness, and decreased rate of pH decline. Although in generation 8 the LMC line did not differ from the RBC line for DL, previous unpublished data have shown differences (Table 3). Further generations of selection may be needed to adequately separate the LMC line from the RBC for DL.

The high heritabilities and response to selection for L* in both the LMC and HMC lines as well as the change in correlated traits such muscle pH and DL suggests that primary breeders could develop a sib-test program using L* as a selection trait as a way to either monitor muscle quality or select for or against muscle quality in pedigree elite lines. Utilization of L* in a primary breeding program could be applied in many ways depending on the desired breeding goals. For example, if a pedigree elite line had PSE- or DFD-like issues then selection for L* in the respective directions could be applied to move the population away from either condition. Otherwise, stabilizing selection could be applied to remove extreme families that are producing DFD or PSE-like meat as a way to create stabilization and uniformity in the lines.

To better understand the factors contributing to muscle color, divergent lines were developed. These resource populations will provide a consistent source of genetic material to explore the environmental conditions that contribute to its incidence. It is through this work that true genetic and environmental triggers of undesirable muscle quality can be exposed.

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