Assessing MHC-B diversity in Silkie chickens

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ABSTRACT The major histocompatibility complex (**MHC**) is a highly polymorphic region on chromosome 16, which contains numerous immune response genes, and is known to influence disease susceptibility and resistance in chickens. Variability of MHC-*B* haplotypes in various well-known and commercially utilized breeds has previously been identified. This study aims to understand MHC-*B* diversity in the Silkie breed using a high-density SNP panel that encompasses the chicken MHC-*B* region. DNA was obtained from 74 females and 27 males from a commercial Silkie breeder colony that is maintained through minimal genetic selection practices. A previously described panel of 90 SNPs, all located within the MHC-*B* region, was used to evaluate MHC-*B* variability in the commercial Silkie breeder colony. MHC-*B* haplotypes identified from the individual SNP information in the Silkie colony were compared to published haplotypes from the same region. Of the 27 haplotypes identified in the Silkie population, 8 have been previously described. Nineteen haplotypes are unique to the Silkie population and include one novel recombinant and 2 additional possible novel recombinants. Six haplotypes were found at a frequency greater than 5% of the population, of which 4 are novel. Finally, Hardy Weinberg Equilibrium (**HWE**) was calculated for the observed haplotypes, which were found to be in HWE. This study shows considerable MHC-*B* diversity in the Silkie breed and adds further information on variability of the MHC-*B* region in the chicken.

Key words: Silkie, MHC-*B*, haplotype, SNP

2020 Poultry Science 99:2337–2341
https://doi.org/10.1016/j.psj.2020.01.005

INTRODUCTION

Silkies are an archaic and unique breed. Early accounts of chickens with "cat fur" were reported in China in the 12th century (Haw, 2006). Silkies were recognized as the first United States Poultry Standard of Perfection published in 1874 (Haw, 2006; Ekarius, 2007; Hu et al., 2010). The breed is distinguished by fine silken feathers resembling hair, with feathering down the legs, rose comb, and polydactyly (Hutt, 1949; American Poultry Association, 2001; Haw, 2006). The breed standard accepts feather coloration of white, black, buff, blue, gray, and partridge. The breed is historically significant as it has been, and currently is, highly valued for its medicinal qualities in Asian communities (Bliss, 2011; Higginbottom et al., 2018).

The most striking physical feature of the Silkie breed is the internal and external melanin pigmentation present throughout the body. Bateson and Punnett (1911) initially hypothesized that the coloration was a result of a pigmentation and an inhibition factor. Dorshorst et al. (2010) mapped the skin pigment associations to 2 main genes, an inhibitor of dermal melanin (*Id*) on chromosome Z and fibromelanosis (*Fm*) on chromosome 20, using a genome-wide single-nucleotide polymorphism trait association. SNP regions associated with other traits observable in Silkies were identified, including polydactyly on chromosome 2, hook-less feathers on chromosome 3, and feathering of the legs on chromosome 13 (Dorshorst et al., 2010). The Silkie chicken has served as a scientific model organism for identifying neural crest cell migratory pathways and proliferation throughout embryogenesis due to the melanism coloration (Lecoin et al. 1994; Reedy et al., 1998; Faraco et al., 2001). From a production standpoint, Silkies represent a minor portion of the meat bird industry in the United States; however, production of the breed has remained consistent due to specialized markets in ethnic areas, such as Los Angeles and San Francisco (Loper, unpublished).

The chicken major histocompatibility complex (**MHC**) comprises 2 independently assorting regions, the MHC-*B* and MHC-*Y* regions, both of which are

Received September 23, 2019.
Accepted January 1, 2020.

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found on chromosome 16 (Briles et al., 1993; Miller et al., 1996). The recent review of Miller and Taylor (2016) summarizes the current knowledge of these 2 genomic regions. The MHC genotype information presented herein encompasses the MHC-*B* region only.

The highly polymorphic MHC-*B* region contains multiple genes associated with chicken immune function. Numerous studies have shown strong associations between variation within the chicken MHC-*B* and disease resistance. Research has been done evaluating associations with the MHC-*B* to response to viral diseases such as Marek's disease (Goto et al., 2009), Rous sarcoma virus (Taylor, 2004), and Newcastle disease virus (Norup et al., 2011). The chicken MHC-*B* region is also known to influence the outcome of numerous bacterial diseases including those induced by *Staphylococcus aureus* (Cotter et al., 1992), *Escherichia coli* (Macklin et al., 2002, 2009; Cavero et al., 2009), and *Salmonella enteritidis* (Schou et al., 2010). Association of MHC-*B* haplotypes with resistance to internal and external parasites has also been found (Lillehoj et al., 1988; Owen et al., 2008; Schou et al., 2010). Furthermore, the chicken MHC-*B* has been shown to be associated with economically relevant traits in production systems including body weight, mortality, egg production, and hatchability (Bacon, 1987; Abplanalp et al., 1992; Sander, 1993).

It has been suggested that it is the heterozygous nature of this highly polymorphic region that has the greatest impact on overall disease resistance (Sato et al., 1992). Ngeno et al., (2015) indicated that a high level of genetic diversity in the MHC-*B* region of indigenous chicken populations in Kenya is reflective of the hardy nature of the chickens. Izadi et al., (2011) showed that 4 noncommercial flocks (Taiwanese Cross, Yellow Wai-Chau, Shiqi, and Yellow Shiqi) contain more variability at the LEI0258 microsatellite marker within the MHC region, when compared to 2 intensively selected commercial flocks. The authors hypothesized that the high MHC variability in these pasture, or free range–raised, noncommercial flocks would likely translate to more effective disease resistance, as these populations were developed under stressful environments (parasite/disease exposure). Alternatively, reports have indicated homozygotes or heterozygotes could demonstrate advantageous performance in certain haplotype combinations in hybrid progeny (Dunnington et al., 1992). Examination of MHC-*B* variability in a wild sampled Red Jungle Fowl population revealed extensive heterozygosity (Nguyen-Phuc et al., 2016). Ultimately, variability of the region itself, in addition to specific gene variations, may lead to enhanced immune functionality of an individual.

The sequence of a 243,833 bp reference region in the chicken MHC-*B* provides the opportunity to standardize haplotype identification based on DNA variation (Shiina et al., 2007). A SNP panel that encompasses most of the MHC-*B* region, developed by Chazara et al. (2010), was subsequently modified to cover 230,000 bp with 101 SNP (Fulton et al., 2016b). Some of these SNPs are within a region that includes gene duplication and deletion, and thus, accurate genotyping for those particular SNP can be difficult. The genotypes presented herein encompass the MHC-*B* region from SNP MHC-J06 to MHC-178 as defined by Fulton et al. (2016b) and covers 210,000 bp. The SNP panel was initially validated using DNA of known serologically defined MHC haplotypes from multiple research lines, as well as standard breeds, heritage breeds, and elite commercial egg production lines from multiple sources. Subsequently, additional haplotypes have been identified in Finnish Landrace populations (Fulton et al., 2017) and an Argentinian Campero population (Iglesias et al., 2019).

Owing to the economic value and cultural significance of the Silkie breed, evaluation of genetic variation is warranted. The association of the MHC-*B* region of the chicken with disease resistance suggests that understanding the genetic variation within Silkies has relevance to disease resistance and potential improved value of the breed. Furthermore, additional information on haplotype variation existing within different breeds provides insight of variation within this important region of the chicken genome.

METHODS

Study Population

One hundred one individuals were randomly selected from a closed Silkie colony (74 females and 27 males). The 5,000-head commercial breeding colony is white feathered and is used for producing offspring for specialty poultry meat markets. The colony is maintained through minimal genetic selection practices. The only parameter used is selection against red-colored combs, as black combs are preferred in the consumer meat market. A comb color other than black, or dark mulberry, is not ideal according to the breed standard, and a red comb is considered a disqualification (American Poultry Association, 2001). This work was completed under the approved Institutional Animal Care and Use Committee application on the Fresno State campus (#167).

Blood Collection and Genotyping

10 μL of blood was transferred onto a Whatman FTA Elute card (GE Healthcare Bio-Sciences Corp., Piscataway, NJ) and allowed to dry overnight. The DNA extraction procedure followed the manufacturer's instructions. Genotyping was completed on the 90 SNP panel (MHC-J6 to MHC-178) using KASP (LGC Biosearch Technologies, Middlesex, UK) genotyping procedures (subset of the 101 SNP panel) described in Fulton et al. (2016b). Briefly, the KASP technology uses PCR-based single SNP assays with allele-specific competitive amplification, and fluorescence-based end-point reads (Semagn et al., 2013). Any PCR-based technology will work for detection of the alleles, if the primer sequences are known. Details, including the specific primers for each assay, are given in the study by Fulton et al., 2016b. Genotypes were

determined using Kraken software (LGC Biosearch Technologies, Middlesex, UK).

Defining and Naming Haplotypes

Haplotypes were identified following a two-step process as described in the study by Fulton et al. (2017). Homozygous individuals for all SNPs were identified and used to establish an initial set of haplotypes. Heterozygous individuals were then compared with these initial haplotypes and used to identify additional alternative haplotypes present in the population within heterozygote individuals. Finally, each haplotype found was compared to common haplotypes reported in previous studies using the same SNP panel (Fulton et al., 2016a,b; Fulton et al., 2017, Iglesias et al., 2019) to determine if the haplotypes had been previously reported or were novel.

Segregation of haplotypes identified in the Silkie population was evaluated for Hardy-Weinberg Equilibrium (**HWE**) by calculating the frequency of the parental haplotypes. Calculated expected counts were compared with observed frequency through a chi-square test. All rare haplotypes (frequencies less than 5%) were grouped together for this analysis.

RESULTS AND DISCUSSION

A total of 27 haplotypes were identified in the Silkie population under study, and the genotypes obtained for each SNP are given in Figure 1. Comparison of these haplotypes with those previously identified within standard breeds, heritage breeds, and commercial egg production breeds (Fulton et al., 2016a) showed that 8 of these haplotypes (43%) had been previously identified. Comparison with the information from the original source of these 8 haplotypes indicates that 7 were previously found in the Rhode Island Red (**RIR**), White Plymouth Rock (**WPR**), Barred Plymouth Rock (**BPR**), and/or New Hampshire (**NH**) breeds. This suggests that there may have been some historic introgression of these specific breeds in to the Silkie breed, perhaps to improve meat production. This hypothesis would need to be tested with a more thorough examination of genomic diversity outside of the small segment of chromosome 16 that contains the MHC-*B* region that was the focus of this study.

The SNP composition of the remaining 19 novel haplotypes is also provided in Figure 1. Comparison of these 19 novel Silkie haplotypes with novel haplotypes reported in the Finnish Landrace (Fulton et al., 2017) and Argentinian Campero (Iglesisa et al., 2019) showed no shared haplotypes, and thus, these are unique to the Silkie population evaluated in this study. Alignment of BSNP-SLK-Hap13 with the other haplotypes found within the Silkie population shows identical SNP genotypes with BSNP-O03 for the first 64 SNPs, followed by identical SNP genotypes with BSNP-SLK-Hap01 for the last 27 SNPs. This commonality suggests that the novel Silkie haplotype BSNP-SLK-Hap13 may be recombinant between the BSNP-O03 haplotype (from SNP MHC-J6 to MHC-118) and the BSNP-SLK-Hap01 (from MHC-118 to MHC-178), with the recombination event having occurred between SNP-MHC116 (149,999 bp) and MHC-119 (157,474 bp). Recombination events in this same region have been previously reported (Fulton et al., 2016b).

Two additional potential recombinants were also found. BSNP-SLK-Hap02 and BSNP-SLK-Hap03 each can be explained by potential recombination events between other haplotypes present in the Silkie population. For both of these novel Silkie haplotypes, there is a large swath of the MHC-*B* region identical with other haplotypes, making it difficult to define a recombination region. Possible parental MHC-B haplotypes for each of these potential recombinants are given in Figure 1. It is also possible that the actual parental haplotypes are not represented in this particular population sampling. All of these recombinants are merely proposed based on the limited information available. Confirmation or refuting of these proposed parental haplotypes could happen if additional MHC-B SNP typing was done for the entire colony. It is

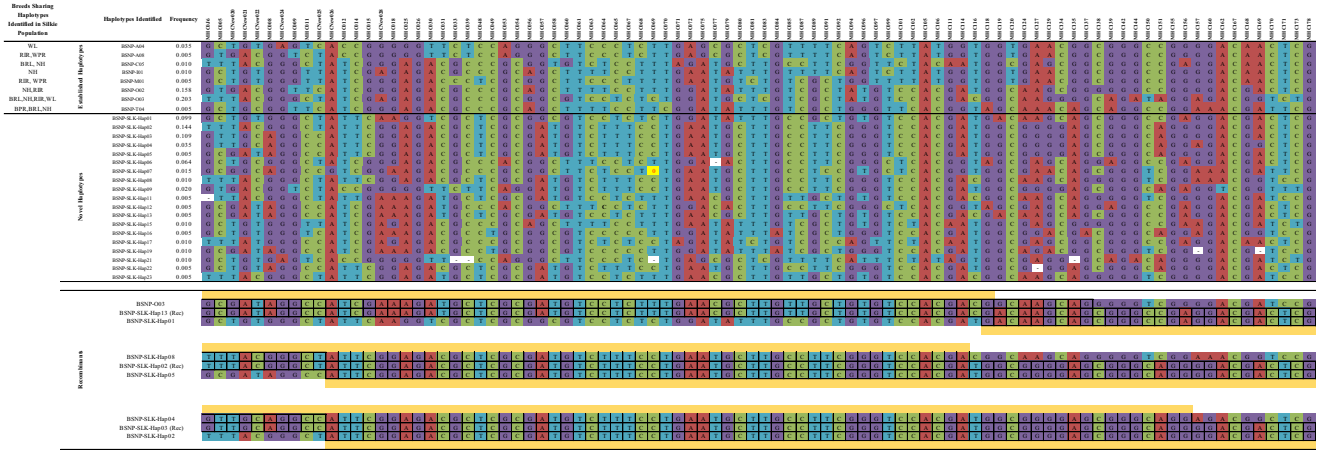

Figure 1. Existing and novel haplotypes identified in the Silkie population. Recombinant and possible recombinants are also listed.

also possible that the original parental haplotypes for these novel recombinants no longer exist in the population.

The number of BSNP haplotypes identified within this sampling of 102 birds is considerably higher than that found for other randomly mated population breeds with similar sample sizes. The pure breeds studied by Fulton et al. (2016a) had only 1 to 4 BSNP haplotypes per breed, which was likely a consequence of a historic genetic bottleneck for those pure breeds. By contrast, the heritage broiler populations, which were each initially formed from multiple line crosses, had 5-11 BSNP haplotypes per population. This is much less than the 27 haplotypes found in the Silkie population. Two of the haplotypes from the heritage broiler populations, BSNP-C05 and BSNP-T04, were also found in the Silkie breed. The Argentina Campero chicken synthetic breed was developed by crossing multiple established breeds and was found to contain 11 BSNP haplotypes, sharing BSNP-A08 and BSNP-M01 (both initially found in RIR and WPR breeds) with the Silkie population (Iglesias et al., 2019).

Seven of the haplotypes found within the Silkie population are shared with the New Hampshire, Rhode Island Red, and White Leghorn breeds. These breeds also share the most frequent haplotypes found in 13 Finish Landrace populations evaluated by Fulton et al. (2017). It was speculated that the similarity in haplotypes among the NH, RIR, WL, and Finish populations may be due to similar breeding histories between Finnish Landrace and highly selected production breeds (Fulton et al., 2017). Interestingly, seven of the 13 Finnish Landrace populations evaluated using the SNP panel described in Fulton et al. (2016b) share haplotypes with the Silkie population.

When considering the haplotype counts from the 101 Silkie individuals evaluated, 6 haplotypes were found at greater than 5% frequency. Two of these are established haplotypes, and 4 are novel. The most frequent haplotype found in the Silkie population is the BSNP-O03 haplotype (20.3%), which was previously found in 4 breeds (BRL, NH, RIR, and WL). The BSNP-O02 haplotype was at a frequency of 15.8% and was previously seen in 2 other breeds (NH, RIR). The third most prevalent haplotype is the novel SLK-Hap02 at 14.4%. Both novel and established haplotypes in the population were found at low frequencies (<5%). The remaining 21 haplotypes were found at less than 3% in the population, and in many cases, only one individual was identified with that haplotype. More haplotypes were identified within the Silkie population than have been previously reported in individual populations (Fulton et al., 2016a, 2017; Iglesias et al. 2019), with the exception of the considerably diverse MHC region in wild caught jungle fowl (Nguyen-Phuc et al., 2016).

It is worth noting that the shared haplotypes were previously reported in breeds common to North America used for egg production, meat, or dual purpose. The haplotypes within the population were determined to be in HWE, as was expected in this closed population of random mated individuals ($P > 0.05$).

Commercial Silkie production represents a culturally significant minor poultry production industry in the United States (Chen and Weijian, 1998; Li et al., 2004; Higginbottom et al., 2018). Understanding genetic diversity within the commercial population, especially as it relates to the immune-important MHC region, is warranted. Interestingly, the Silkie population evaluated has shown to be highly variable within the MHC-*B* region, compared to other populations evaluated. It is likely that this genetic diversity beneficially impacts the immune function of this population. Finally, information from this Silkie population adds to the growing collection of MHC data using the SNP panel. The information described here is best understood within the context of other data gathered using this SNP panel, which aims to realize, and quantify, the variation of the polymorphic MHC in the chicken.

ACKNOWLEDGMENTS

The authors are appreciative of Pitman Family Farms for providing access to samples for this study and to Ashlee Lund and the Hy-Line International Molecular Genetics Lab for providing the genotyping.

Conflict of Interest Statement: The authors declare that they have no conflict of interest.

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