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Serological Screening for MHC (B)-Polymorphism in Indigenous Chickens

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ABSTRACT

As part of a series of studies to characterize innate and specific immune responses of indigenous chicken lines, birds from Bolivia and India were screened serologically for MHC class IV (BG) polymorphism by direct haemagglutination using haplotype-specific antisera (B2, B4, B12, B13, B14, B15, B19, B21). The sample consisted of 95 Bolivian indigenous chickens and 119 hens from the four most common North Indian 'back-yard' chicken lines: Yellow Aseel (AP), Kadaknath (KN), frizzled typed (Ff^-) and naked neck (NN). Of all chickens tested, the majority were haplotyped as B2, B15, B19 and B21. Of the Bolivian chickens, 89.5% could be haplotyped: 54.9% were homozygous (including 43.3% B15), and 34.6% were heterozygous (including 15.7% B15). B2-like haplotypes were not found among the Bolivian hens, and only 3.2% of these birds showed homozygous B21-like proteins. Of the Indian hens, MHC (BG)-like proteins could be detected in 60.0% of the AP birds, 6.7% of the KN birds; 40.0% of the Ff^- birds; and 10.3% of the NN birds. In these lines, a total of 40.1% (AP), 6.7% (KN), 30.1% (Ff^-) and 10.3% (NN) were homozygous for the B-haplotype. Only in the AP line (19.9%), and the Ff^- line (9.9%) were heterozygous B-haplotypes types found. The B2 haplotype was found in all Indian chicken lines. Most Indian birds have completely unknown haplotypes, indicating a potentially interesting genetic pool. Subgrouping the Bolivian and Indian indigenous hens into monomorphic BG populations revealed individual differences based on the B-types.

Keywords: chicken, indigenous, Bolivia, India, MHC-haplotyping

Abbreviations: CATT, Card Agglutination Test for Trypanosomiasis; CRBC, chicken red blood cells; HA. haemagglutination; PBS, phosphate-buffered saline; SRBC, sheep red blood cells; MHC, major histocompatibility (BG) complex

INTRODUCTION

The chicken major histocompatibility complex (MHC), or B complex, consists of several clusters of highly polymorphic genes. The class I (BF) and class II (BL) antigens resemble their mammalian counterparts in the encoded protein structure, whereas the class III region has been proposed as the 'primordial immune complex' (Salter-Cid and Flajnik, 1995). The class IV (BG) region encodes the B blood group antigens. There is a low crossing-over (1:2000) between BG and BF/BL genes in

European chickens (Hala *et al.*, 1981; Plachy *et al.*, 1992a,b). Two of the MHC genes (BF and BG) code for glycoproteins, which are expressed on the surface of red blood cells. The amount of BG antigen present on erythrocytes is several times greater than the amount of BF antigen. BG antigens can be detected by direct haemagglutination (HA) using appropriate alloantisera, identifying different MHC types (Lamont, 1991, 1998b). HA has the advantage of speed and ease. Besides the MHC complex, chickens also have an Rfp-Y-system (Guillemot *et al.*, 1988; Miller *et al.*, 1994). However, identification of Rfp-Y (MHC-like) haplotypes seems of minor importance (Pharr *et al.*, 1996, 1997).

Chickens have a small compact polymorphic MHC, which may have been stripped down to the essentials during evolution (Kaufman and Wallny, 1996; Kaufman *et al.*, 1999). Genetic resistance to diseases is a multigenic trait and occurs through a network of mediator proteins such as the molecules of the major histocompatibility complex. The diversity of these proteins, due mainly to intrinsic polymorphism of the genes, causes phenotypic variation in disease resistance (Cole, 1968; Longenecker *et al.*, 1976). There are a number of mainly viral diseases for which resistance and susceptibility are determined by particular chicken MHC haplotypes (Kaufman and Wallny, 1996), such as the well-known linkage of chicken MHC polymorphism and resistance to Marek' s disease (Lamont, 1998a; Juul-Madsen *et al.*, 2000; Kaufman, 2000).

Studies of the MHC (B) in chickens are essential for understanding immunocompetence to many avian pathogens. European and American economically important breeds have become standard reference stocks for MHC (B) haplotyping. This is mainly due to the interest in identification of genetic and immunological markers that could be used in breeding programmes to improve immune competence and production. Thus, 'standard' haplotypes are almost all derived from the White Leghorn. However, preliminary typing of other (indigenous) breeds of chickens, and of wild chickens, indicates the existence of a much wider spectrum of allomorphs (Simonsen *et al.*, 1982) and reveals new alleles, often with distinct haplotypes (Hepkema *et al.*, 1991; Pinard *et al.*, 1993; Briles *et al.*, 1993; Li *et al.*, 1999; Livant *et al.*, 2001). Since each class of MHC genes is a potential candidate for a role in disease resistance (Nordskog *et al.*, 1987; Lamont, 1998a) and immune response (Fulton *et al.*, 1996), knowledge of the B system of poultry should not be limited to White Leghorns.

Chickens used in traditional poultry in developing countries are of great importance to village households, but unfortunately are often neglected by avian researchers. For instance, little is known on the distribution of B-haplotyes in indigenous chickens and possible similarities of their MHC products with those of the commercial stocks. Indigenous flocks are small, scattered, multi-aged and under minimal control. One of the major constraints to indigenous chicken production is undoubtedly the existence of various diseases, with the most significant causes of mortality being Newcastle disease; infectious bursal disease, fowl pox, ectoparasitism and endoparasitism. Furthermore, birds are almost never vaccinated. These populations continue to survive in potentially hostile environments, for generation after generation. Thus it is worthwhile to examine the distribution and subsequently the contribution of the B system to disease resistance in this type of 'natural' population. In earlier studies we described different levels and

activation of innate (classical and alternative complement pathways) and specific immune responses (antibody titres to SRBC) in a variety of indigenous chicken lines (ecotypes) worldwide. Low complement levels and complement responses as well as specific antibody responses were found in Bolivian ecotypes, compared with various Indian ecotypes (Baelmans *et al.*, in press a,b). Also, different complement levels were found in commercial lines related to the BG type (Parmentier *et al.*, 2004). In the present study, BG polymorphism was studied in several indigenous chicken populations, using a panel of standard White Leghorn-derived BG-specific alloantisera.

MATERIALS AND METHODS

Chickens

One hundred and nineteen hens from the four most common North Indian 'back-yard' chicken lines were examined. Hens were housed at the Central Avian Research Institute (CARI, Izatnagar, India). The following lines were studied: the Yellow Aseel, an indigenous 'fighting' breed from Andhra Pradesh (AP: $n = 30$); the Kadaknath, a famous Indian indigenous breed used for medicinal purposes in tribal areas (KN: $n = 30$); the Indian frizzled type (Ff^{-}: $n = 30$); and the Indian naked neck broiler type (NN: $n = 29$) chickens. In Bolivia, 95 back-yard chickens from Andean regions were analysed for BG haplotypes. Birds were kept at the University of Oruro (Universidad Technica de Oruro, Bolivia).

Blood collection

Blood (2 ml) was collected by wing vein puncture into ice-cold glass tubes containing 0.5 ml ACD solution (13.2 g trisodium citrate dihydrate, 4.8 g citric acid, 14 g glucose per litre H_2O). Blood samples were washed three times in phosphate-buffered saline (PBS), pH 7.2. Chicken red blood cells (CRBC) were used as a 2% packed volume in PBS.

MHC haplotyping

Hens were serologically haplotyped for MHC (BG and BF) by direct HA with alloantisera on a CATT card (Card Agglutination Test for Trypanosomiasis) as follows. After mixing, 50 µl of 2% CRBC and 50 µl of diluted antiserum were incubated in a test area for 30 min at room temperature in a humidified atmosphere. Then, 50 µl of sterile 1:5 diluted chicken plasma in PBS was added to each area. After 30 min of incubation, CATT cards were rotated gently while tilting the card. Strong or moderate agglutination of CRBC could occur, or a negative reaction (no agglutination). All alloantisera were raised by weekly intramuscular alloimmunizations, screened in serial dilution against animals from the population, and were made

specific, if necessary, by appropriate absorption. A non-specific cross-reactive alloantiserum (CR), binding to different MHC (B) haplotypes from Red Jungle Fowl, Brown Leghorn and Scandinavian White Leghorn, was included in the HA test panel (Table I).

TABLE I
MHC (B) test panel used for haplotyping indigenous hens

B-G			12			15	19	21	CR
B-F	2	4	12	13	14	15	19	21	

Subtyping

Reagents for serological analysis of MHC polymorphism in chickens other than White Leghorns are sometimes not adequate for testing indigenous chickens. In practice, one can reduce the nuisance of cross-reactive antisera, to a degree of group-combinations, by absorption procedures. In the end, monomorphic BG populations can be determined in field chickens to separate/segregate and link them into groups. A particular group of specific MHC (B) haplotyped hens from each line were tested for possible segregation into smaller groups after analyses of absorption patterns with other CRBC B types and binding with the CR reagent.

RESULTS

A total of 91.6% of the native Bolivian chickens were categorized for known MHC (B) haplotype-like proteins (i.e. positive for CR and/or MHC (B) reagents tested). Only 2.1% of the Bolivian birds had some homology with known MHC (B) haplotypes (i.e. they were positive for CR but not for MHC (B)) and 8.4% of the indigenous chickens from Bolivia had unknown haplotypes, i.e. they could not be detected by CR or specific MHC (B) reagents. A total of 54.6% of the indigenous hens from India could be categorized for known MHC (B) haplotype-like proteins, whereas of the Indian birds, 45.4% had possible unknown haplotypes (Table II).

A total of 54.9% of the Bolivian chickens were categorized as homozygous and 34.6% as heterozygous MHC (B) haplotype. In the four Indian breeds, variable amounts of respectively homozygous and heterozygous MHC (B) haplotypes were found: 40.1% and 19.9% for the AP line; 30.1% and 9.9% for the Ff^{-} line; 10.3% and 0% for the Indian NN line; and only 6.7% of the KN line were homozygous for the MHC (B) haplotype (Table III).

Haplotype B2-like protein was not found in the Bolivian hens; a few (3.2%) had a B21 homozygous haplotype, whereas 29.4% of the Bolivian chickens were heterozygous for B21. Of the haplotyped indigenous hens from Bolivia, 43.3% were homozygous for B15, and 15.7% were heterozygous for B15. From the MHC (B) typed

TABLE II
Haemagglutination indices for CR and MHC (B) typing of hens from Bolivia and India

CR	MHC (B)	Bolivia (n = 95)	India (n = 119)
Positive	Positive	22.1%	12.6%
Positive	Negative	2.1%	25.2%
Negative	Positive	67.4%	16.8%
Negative	Negative	8.4%	45.4%

Indian chickens, the majority (30.1%) of the B2 haplotype was found in the AP line, whereas B21 was more present in the Ff^- line (20.1%). A total of 93.3% of the chickens from the Indian KN line could not be categorized for known MHC (B) haplotype-like proteins with the current panel of alloantisera. Only 6.7% could be MHC (B) haplotyped, being B2. Most of the chickens (89.7%) from the NN line could not be categorized for known MHC (B) haplotype-like proteins with the present alloantisera. Only 6.9% (B2) and 3.4% (B15) could be MHC (B) haplotyped. In the Ff^- line, 40% had some homology with known MHC (B) haplotypes, consisting of a mixture of B2, B12, B14, B19 and B21; B15 was not detected. The variety in the AP line was even larger than in the Ff^- line (Table III).

Using CR alloantisera, more positive agglutination was found in the Indian lines, with respectively 60.0% (AP), 33.3% (Ff^-), 24.1% (NN), and 33.3% (KN) of the blood samples tested.

When subtyping the Bolivian chickens into a monomorphic B21 BG population by means of absorption assays, it appeared that, in the group of 36 hens selected, 18 different groups could be formed containing various individuals (Table IV). From the 36 subgrouped Bolivian hens, 18 were homozygous for a certain MHC (B)-like protein, and 18 were heterozygous. When subgrouping the Indian hens, the AP line revealed four different groups. In the NN line, the five individuals were grouped into three groups. Following the HA reaction pattern of the Ff^- line, the five hens could be grouped into possible three different groups, but the same birds could probably also be catalogued as one group (data not shown).

DISCUSSION

Indigenous Bolivian chickens were screened serologically for MHC (BG) polymorphism. A surprisingly high percentage (89.5%) of them could be serotyped for specific MHC (BG) haplotypes, due to the presence of 43.3% of homozygous B15 and 10.5% of heterozygous B15 haplotypes. With respect to the high-altitude habitat of these birds

TABLE III
MHC (BG) polymorphism (%) from indigenous hens from Bolivia and India

			India (n = 119)			
		Bolivia (n = 95)	AP line (n = 30)	Ff$^-$ line (n = 30)	NN line (n = 29)	KN line (n = 30)
CR		24.2	60.0	33.3	24.1	33.3
MHC (B) homozygous	B2	0	16.8	3.3	6.9	6.7
	B4	0	3.3	0	0	0
	B12	0	6.7	10.0	0	0
	B14	0	0	3.3	0	0
	B15	43.3	3.3	0	3.4	0
	B19	8.4	6.7	0	0	0
	B21	3.2	3.3	13.5	0	0
MHC (B) heterozygous	B2B4	0	3.3	0	0	0
	B2B19	0	6.7	3.3	0	0
	B2B21	0	3.3	3.3	0	0
	B12B21	0	3.3	0	0	0
	B15B21	10.5	0	0	0	0
	B15B19	5.2	0	0	0	0
	B19B21	18.9	3.3	3.3	0	0
Specific MHC (B) unknown		10.5	40.0	60.0	89.7	93.3

TABLE IV
Subgrouping of chickens from Bolivia and India into monomorphic BG population by means of absorption assay

	Bolivia (n = 36)				India (n = 15)				
					AP line (n = 5)		NN line (n = 5)		Ff$^-$ line (n = 5)
Groups	8	4	4	2	3	1	2	1	1
No of individuals	1	2	3	4	1	2	1	3	5

and its correlated risk for ascites and the absence of risk of avian pathogenic diseases, which is minimum at this altitude, B15 has been selected as the dominant MHC (B) type. Only a minority (3.2%) were B21-like. The B2 haplotype was not detected within the Bolivian chickens. These data may possibly also be related to a low infectious disease pressure. The second set (cross-absorption) in search of polymorphism of B-haplotypes in indigenous hens from Bolivia revealed that the population consisted of a variety of individuals: i.e. from the 36 hens, 18 different groups could be formed. Previously we found low levels and activation of both classical and alternative complement pathways, and specific antibody titres directed to SRBC in the Bolivian birds (Baelmans *et al.*, in press a.b).

Indigenous Indian hens were divided into four different indigenous 'lines'. The Yellow Aseel (AP) and Kadaknath (KN) lines represent homogeneous phenotypes: muscled and black, respectively. The Indian heterozygous naked neck (NN) line and the group with frizzled characteristics (Ff^{-} line) consist of major gene phenotypic characteristics. As expected, only 6.7% of the Kadaknath ('black bird') chickens could be haplotyped. In the hens from the NN line only homozygous B2 and B15 haplotypes were found; however, 89.7% of the birds could not be typed with the present alloantisera. Even with the CR alloantisera, only 24.1% had MHC (B)-like proteins. In hens from the AP line, the highest amount of B2 (16.8%) was found, whereas the presence of B15 is minimal in both the AP line (3.3%) and the NN line (3.4%). The majority of the indigenous Indian hens thus have completely unknown MHC (B) haplotypes, reflecting a potentially interesting genetic pool.

Of the eight different MHC (B) alloantisera used, it appeared that results of the HA typing depends largely on the chicken population tested. This suggests that MHC haplotyping of non-commercial indigenous chickens awaits the development of new, probably molecular, reagents and approaches. The general appearance of only a few haplotypes (B2, B15 and B21) may reflect the importance of these haplotypes. The B2 and B21 haplotypes derived from White Leghorns (Bacon and Witter, 1992, 1994a,b) and B21-like haplotypes in Brown layers (Hepkema *et al.*, 1991; Pinard and Hepkema, 1993; Pinard *et al.*, 1993; Parmentier *et al.*, 2002) are generally associated with enhanced immune competence and enhanced disease resistance. The B15 of White Leghorns is often related to enhanced disease susceptibility (Bacon and Witter, 1992, 1993). The B13, also 'known' for enhanced disease susceptibility, could not be detected in the back-yard hens tested.

Obtaining knowledge of the MHC haplotypes of indigenous chickens, which depend mainly on their genetic resistance to infectious diseases, may add considerably to enhancement of the health of poultry and the incorporation of 'resistance' genes into the current commercial lines. The presently available serological reagents, however, are not sufficient to study MHC polymorphism in indigenous chickens. Since relatively high levels of innate and specific immune responses, comparable to commercial lines, can be detected in Indian ecotypes (Baelmans *et al.*, in press a,b), knowledge of their MHC would add to an improved understanding of mechanisms underlying natural disease resistance.

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Dépistage sérologique du polymorphisme MHC (B) chez les poulets indigènes

Résumé – Dans le cadre d'une série d'études visant à caractériser les réponses immunitaires innées et spécifiques de lignées de poulets indigènes, des poulets de Bolivie et d'Inde ont fait l'objet d'un dépistage sérologique du polymorphisme MHC de classe IV (BG) par hémagglutination directe en utilisant des antisérums spécifiques aux haplotypes (B2, B4, B12, B13, B14, B15, B19, B21). L'échantillon a consisté en 95 poulets indigènes boliviens et en 119 poulets provenant des quatre lignées de poulets d'arrière-cour nord-indiens les plus fréquemment rencontrées: Yellow Aseel (AP), Kadaknath (KN), de type frisé (Ff^{-}) et cou nu (NN). Sur tous les poulets testés, la majorité a été haplotypée comme étant de type B2, B15, B19 et B21. Parmi les poulets boliviens, 89.5% ont pu être haplotypés: 54.9% étaient homozygotes (dont 43.3% d'haplotypes B15) et 34.6% étaient hétérozygotes (dont 15.7% d'haplotypes B15). Des haplotypes apparentés au type B12 n'ont pas été retrouvés parmi les poulets boliviens et uniquement 3.2% de ces poulets ont manifesté des protéines homozygotes apparentées à l'haplotype B21. Parmi les poulets indiens, des protéines apparentées au polymorphisme MHC (BG) ont pu être détectées chez 60.0% des poulets AP, 6.7% des poulets KN; 40.0% des poulets Ff^{-} et 10.3% des poulets NN. Parmi ces lignées, un total de 40.1% poulets (AP), 6.7% (KN), 30.1% (Ff^{-}) et 10.3% (NN) étaient homozygotes pour l'haplotype B. Des haplotypes hétérozygotes de type B ont uniquement été retrouvés dans la lignée de poulets AP (19.9%) et Ff^{-} (9.9%). Des haplotypes B2 ont été retrouvés dans les lignées de poulets indiens. La plupart des poulets indiens avaient des haplotypes complètement inconnus, ce qui est révélateur d'un pool génique potentiellement intéressant. Le sous-groupage des poulets boliviens et indiens en des populations BG monomorphiques a révélé des différences individuelles basées sur les haplotypes de type B.

Análisis de detección serológico para Polimorfismo-MHC (B) en pollos indígenas

Resumen – Como parte de una serie de estudios para caracterizar las respuestas inmunes innatas y específicas de líneas de pollos indígenas, se analizaron serológicamente aves de Bolivia y la India para detectar polimorfismo del Complejo Principal de Histocompatibilidad (MHC) de clase IV (BG) mediante hemaglutinación directa utilizando antisueros específicos de haplotipos (B2, B4, B12, B13, B14, B15, B19, B21). La muestra consistía en 95 pollos indígenas bolivianos y 119 gallinas provenientes de las cuatro líneas de pollos 'de corral trasero' más comunes del Norte de la India: Aseel rubia (AP), Kadaknath (KN), de tipo rizado (Ff^{-}) y de cuello desnudo (NN). De todos los pollos analizados, la mayoría resultó de haplotipos B2, B15, B19 y B21. De los pollos bolivianos, 89.5% podían ser de los haplotipos siguientes: 54.9% eran homocigotos para un gen particular (incluyendo 43.3% para B15), y 34.6% eran heterocigotos para un gen particular (incluyendo 15.7% B15). No se encontraron haplotipos del tipo B2 entre las gallinas bolivianas, y sólo 3.2% de estas aves mostraban proteínas homocigóticas del tipo B21. De las gallinas indias, se podían detectar proteínas del tipo MHC (BG) en el 60% de las aves AP, 6.7% de las aves KN, 40% de las aves Ff^{-}, y 10.3% de las aves NN. En estas líneas, un total de 40.1% (AP), 6.7% (KN), 30.1% (Ff^{-}) y 10.3% (NN) eran homocigóticas para el haplotipo-B. Sólo en la línea AP (19.9%), y en la línea Ff^{-} (9.9%) eran heterocigotas para los haplotipos-B encontrados. El haplotipo B2 se encontró en todas las líneas de pollos indios. La mayoría de las aves indias tienen haplotipos completamente desconocidos, indicando con ello una reserva genética potencialmente interesante. Al subagrupar las gallinas indígenas bolivianas e indias en poblaciones BG monomórficas se revelaron diferencias individuales basadas en los tipos-B.