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A first-generation microsatellite linkage map of the Japanese quail

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Summary

A linkage map of the Japanese quail (*Coturnix japonica*) genome was constructed based upon segregation analysis of 72 microsatellite loci in 433 F₂ progeny of 10 half-sib families obtained from a cross between two quail lines of different genetic origins. One line was selected for long duration of tonic immobility, a behavioural trait related to fearfulness, while the other was selected based on early egg production. Fifty-eight of the markers were resolved into 12 autosomal linkage groups and a Z chromosome-specific linkage group, while the remaining 14 markers were unlinked. The linkage groups range from 8 cM (two markers) to 206 cM (16 markers) and cover a total map distance of 576 cM with an average spacing of 10 cM between loci. Through comparative mapping with chicken (*Gallus gallus*) using orthologous markers, we were able to assign linkage groups CJA01, CJA02, CJA05, CJA06, CJA14 and CJA27 to chromosomes. This map, which is the first in quail based solely on microsatellites, is a major step towards the development of a quality molecular genetic map for this valuable species. It will provide an important framework for further genetic mapping and the identification of quantitative trait loci controlling egg production and fear-related behavioural traits in quail.

Keywords chromosomes, genetic map, Japanese quail, linkage groups, microsatellite

Introduction

The Japanese quail, originally domesticated around the 11th century as a pet song bird (Howes 1964; Crawford 1990), has gained in value as a food animal since 1910 (Wakasugi 1984). Several aspects account for the utility of this bird. First, it has attained economic importance as an agricultural species producing eggs and meat that are enjoyed for their unique flavour. Egg production is paramount in Japan and southeast Asia, while meat is the main product in Europe (Minvielle 1998). Second, the low maintenance cost associated with its small body size (80–300 g) coupled with its short generation interval, resistance to diseases and high egg production, render it an excellent laboratory animal. It has thus been used extensively in many studies including behavioural (Mills & Faure 1991), developmental (Le Douarin *et al.* 1997), physiological (Balthazart *et al.* 2003), genetic (Jones *et al.* 1991) and

biomedical (Ratnamohan 1985) researches. Third, Japanese quail is phylogenetically closely related to the chicken (Stock & Bunch 1982). Both species have a karyotype of $2n = 78$ chromosomes and a similar genome length of 1.2×10^9 bp, consisting of morphologically distinct macrochromosomes (1–8 and the ZW sex chromosomes) and cytologically indistinguishable microchromosomes. Indeed, recent cytogenetic studies have confirmed the highly conserved chromosome homology between Japanese quail and chicken, revealing only very few chromosome rearrangements after divergence of the two species (Shibusawa *et al.* 2001). Thus, the Japanese quail has been recommended as a model species for poultry (Baumgartner 1994; Mills *et al.* 1997).

In poultry, genome research has been concentrated on the chicken, producing a consensus linkage map of nearly 2000 loci (Groenen *et al.* 2000) through international collaboration. Unfortunately, microsatellites, which are the markers of choice for linkage mapping in animals, occur at about a 5–7-fold lower frequency in avian genomes than in mammals (Primmer *et al.* 1997), thus limiting the extent to which marker-rich genetic maps can be developed. In addition, the avian microchromosomes, which are indistinguishable and therefore difficult to map cytogenetically, are

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also gene-dense (Smith *et al.* 2000) and particularly low in microsatellite density (Primmer *et al.* 1997), thus further compounding the problem. Furthermore, cross-species microsatellite amplification in birds, unlike in mammals, is successful only at a low rate even among closely related species (Pang *et al.* 1999; Inoue-Murayama *et al.* 2001), thereby making it difficult to apply markers from a map-rich species. Consequently, mapping is relatively slow in birds, and preliminary genetic maps have only just emerged for the turkey (Burt *et al.* 2003; Harry *et al.* 2003) but are yet to be published for most poultry species.

Until recently, marker information in quail was very scanty and only three classical linkage groups based on plumage colour and blood protein markers (Ito *et al.* 1988a,b; Shibata & Abe 1996; Minvielle *et al.* 2000b) were available. But the situation began to change with the development of original microsatellite markers for quail (Kayang *et al.* 2000, 2002) and the recent publication of the first ever quail genetic map based completely on DNA markers (Roussot *et al.* 2003). This map, which spans 1516 cM and contains 258 loci assigned to 41 linkage groups (including the sex chromosomes), is comprehensive but consists solely of amplified fragment length polymorphism (AFLP) markers. Due to their biallelic dominant nature, the information content of AFLP markers is lower than that of other marker types, especially microsatellites. Besides, AFLP markers are less suited to total genome scan in large populations. Hence, the AFLP map needs to be enriched with other marker types, particularly genes and microsatellites, to enhance its usefulness. As a step towards the development of a quality genetic map for quail, we performed linkage analysis of 72 microsatellites in 10 half-sib quail families and present here a quail genetic linkage map based completely on microsatellite markers.

Materials and methods

Japanese quail resource population

A resource population maintained at the INRA Unité Expérimentale de Génétique Avicole, Nouzilly, France, was used. This population was derived from a cross between two quail lines of different genetic origins (Minvielle *et al.* 2000a). One line was selected for long duration of tonic immobility (Mills & Faure 1991), a fear-related behaviour, and the other line was selected for early egg production (Minvielle *et al.* 2000c). The F_0 generation consisted of 12 dams and 12 sires originating from the two lines, and these were reciprocally crossed to produce the F_1 offspring. Unrelated F_1 matings of 10 males to 30 females generated 10 half-sib families with an average of 43 F_2 chicks each. Thus, a total of 497 quails (24 F_0 , 40 F_1 and 433 F_2) constituted the mapping population from which DNA samples were obtained for genotyping.

The population used for the microsatellite map differed from the AFLP mapping population, which was a cross between two quail lines of the same genetic origin that had been divergently selected for short (STI) or long (LTI) duration of tonic immobility. Although the LTI line was common to both mapping experiments, the F_0 from this line used in our study belonged to a more recent generation of unknown parentage to the AFLP mapping population. The microsatellite mapping population, with the early egg production line, was preferred in our study as it also served in a QTL experiment for production traits and fear-related behaviour.

Microsatellite markers

A total of 103 microsatellite markers were tested of which 100 were original quail microsatellites that had been developed and characterized previously (Kayang *et al.* 2000, 2002). The remaining three were original chicken markers (ADL0037, ADL0142 and ADL0255) located on chicken chromosomes GGA1, GGA6 and GGA4, respectively, that cross-amplify quail DNA and have been confirmed to be orthologous to the quail loci (Inoue-Murayama *et al.* 2001).

Analyses of microsatellite markers

PCR amplifications were carried out on a TAKARA PCR Thermal Cycler (TAKARA Biomedicals, Berkeley, CA, USA) in 15 μ l reaction mixtures containing 20 ng of the DNA template, 0.3 μ M of forward and reverse primers, 130 μ M of each dNTP, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$ and 0.6 U AmpliTaq Gold (Perkin-Elmer, Foster City, CA, USA). After an initial incubation at 95 °C for 9 min, amplification reactions were performed for 30 cycles each with denaturing at 95 °C for 30 s, annealing for 1 min at 48–69 °C depending on the optimized annealing temperature of the primer used, and extension at 72 °C for 1 min. This was followed by a final cycle at 72 °C for 5 min. PCR products of 3–5 markers were combined and electrophoresed simultaneously on an ABI Prism 3100 DNA sequencer (Perkin-Elmer) and analysed using Genescan version 3.7 and Genotyper version 3.7 software (Perkin-Elmer).

Linkage analysis

Linkage analysis was performed using CriMap version 2.4 software (Green *et al.* 1990). Initially, the PREPARE option was used to scrutinize the data for problems with Mendelian inheritance and typing errors were rechecked within Genotyper and corrected where necessary. A two-point linkage analysis of all the markers was then computed based on an LOD score threshold of 3.0. Subsequently, markers belonging to the same linkage group were analysed using the BUILD option and the order of the different loci was

examined with the FLIPS function. Map distances were derived based on the Kosambi mapping function.

Comparative mapping with chicken

Eight markers, which could be shown to be chicken–quail orthologues, were used as an aid to comparative mapping with chicken (Table 1). These consisted of three chicken microsatellites (ADL0037, ADL0142 and ADL0255 located on GGA1, GGA6 and GGA4, respectively) and five quail microsatellites (GUJ0001, GUJ0013, GUJ0023, GUJ0049 and GUJ0063) that cross-amplify chicken DNA and are orthologous to the chicken loci (Kayang *et al.* 2002). The quail cross-species microsatellites were genotyped in the East Lansing chicken reference family (Crittenden *et al.* 1993) and the data analysed by Map Manager Software (Manly 1993) to map the markers on chicken chromosomes. This enabled us to assign some of the quail linkage groups to chromosomes through comparative mapping with the chicken.

Results and discussion

Initially, all 103 microsatellite markers were tested in the F_0 individuals and 12 markers were excluded as uninformative. A further 19 markers were removed from the analysis because of amplification problems or inconsistencies between parental and progeny alleles, thus leaving only 72 markers available for linkage analysis. The number of informative meioses in the mapping population of 497 quail varied from 30 to 754. Fifty-eight markers were resolved into 12 autosomal linkage groups and a Z chromosome-specific linkage group (Fig. 1) while 14 markers were unlinked to any other marker. The linkage groups range from 8 cM (two markers) to 206 cM (16 markers) and the overall map coverage within linkage groups is 576 cM with an average spacing of 10 cM between loci.

Microsatellite markers are ideal tools for the development of genetic linkage maps as evidenced by the steadily growing number of genetic maps based on them. However, one major drawback is that they often tend to have a rather narrow phylogenetic applicability and will typically only work on very closely related species. In our attempt to use chicken microsatellites in quail only 5% (6/121) of the markers successfully amplified orthologous loci in quail and were found to contain microsatellite sequences (Inoue-Murayama *et al.* 2001). Therefore, the first step in a study that uses microsatellite markers is to locate useful markers in the study species. All but three of the microsatellites used in constructing these maps were quail-specific markers.

Of the three chicken markers that amplify orthologous loci in quail (Table 1), two (ADL0037 on GGA1 and ADL0142 on GGA6) were mapped to linkage groups CJA01 and CJA06 (Fig. 1), thus making it possible to assign these linkage groups to chromosomes 1 and 6, respectively (Table 1). The third marker, ADL0255 (GGA4), was however not linked to any other marker in quail. In addition, marker GUJ0013 (linkage group CJA01) was mapped to chicken chromosome GGA1. Thus, the largest linkage group of 16 markers was assigned to chromosome 1 through two cross-species markers, ADL0037 and GUJ0013, of chicken and quail origins, respectively (Fig. 1). These two markers appeared to be very closely linked in quail with a recombination frequency of 1% (LOD score = 22.33). This tight linkage was also observed between the two markers when GUJ0013 was mapped in chicken using the East Lansing reference family, thus raising a suspicion that ADL0037 and GUJ0013 could be the same locus. However, a BLASTN search confirmed that they are in fact different. Similarly, GUJ0063 (linkage group CJA02), GUJ0049 (linkage group CJA05), GUJ0023 (linkage group CJA14) and GUJ0001 (linkage group CJA27) were mapped to chicken chromosomes GGA2, GGA5, GGA14 and GGA27, thereby enabling their respective linkage groups to

Table 1 Assignment of Japanese quail linkage groups to chromosomes through comparative mapping with chicken based on orthologous cross-species markers.

Orthologous marker	Accession number (chicken)	Accession number (quail)	Species of origin	Homology between chicken and quail 5' flank (%)	Chicken chromosome location	Quail linkage group ³
ADL0037	L23912	AF121113	Chicken	95 (105 nt)	GGA1	CJA01
ADL0142	G01567	AF121114	Chicken	91 (116 nt)	GGA6	CJA06
ADL0255 ¹	G01675	AB038402	Chicken	83 (71 nt)	GGA4	–
GUJ0001 ²	AB063261	AB035652	Japanese quail	84 (176 nt)	GGA27	CJA27
GUJ0013 ²	AB063262	AB035823	Japanese quail	86 (91 nt)	GGA1	CJA01
GUJ0023 ²	AB063264	AB035833	Japanese quail	80 (152 nt)	GGA14	CJA14
GUJ0049 ²	AB063268	AB035859	Japanese quail	80 (200 nt)	GGA5	CJA05
GUJ0063 ²	AB063270	AB063131	Japanese quail	86 (138 nt)	GGA2	CJA02

¹Not assigned to any linkage group in Japanese quail.

²Japanese quail originated markers were assigned to chicken chromosomes in this study.

³Japanese quail linkage groups were assigned to quail chromosomes corresponding to the chicken chromosomes on which they were comparatively mapped.

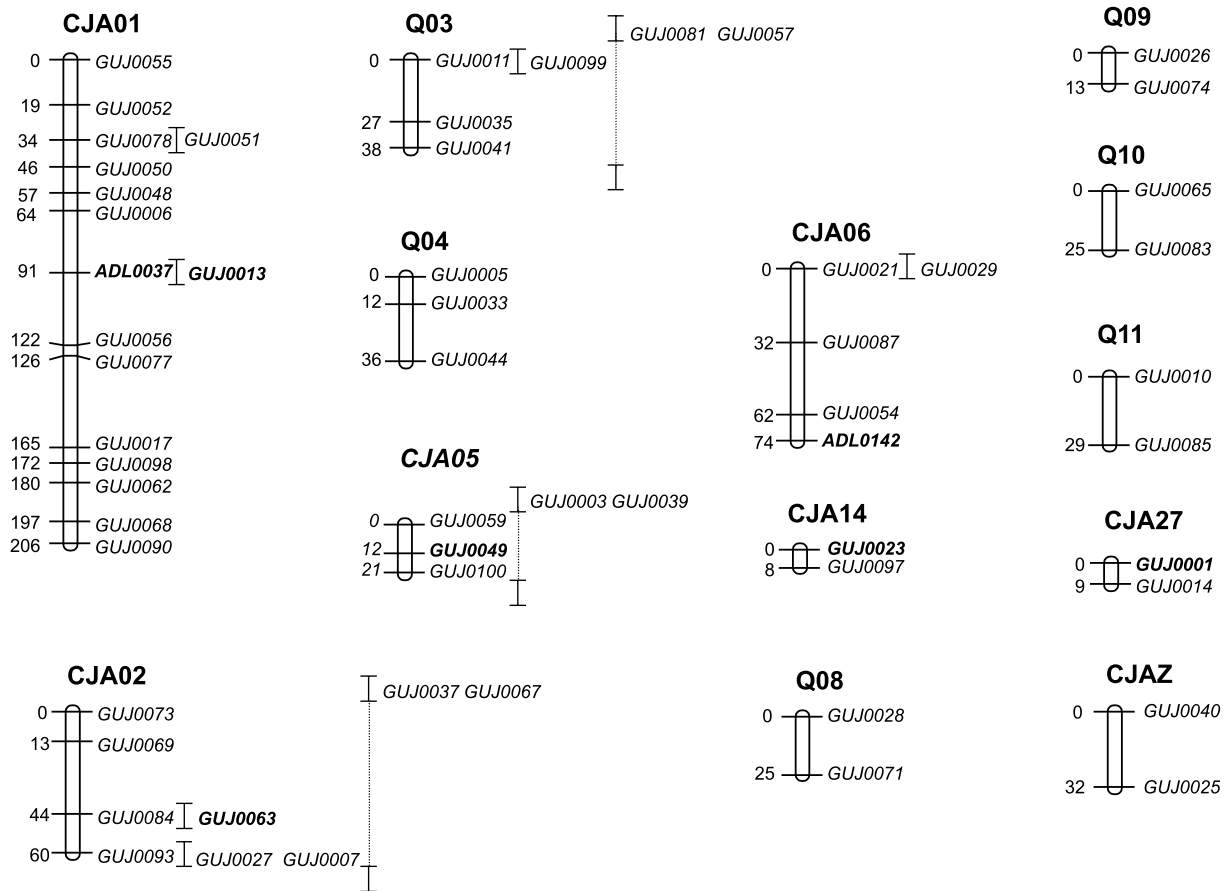


Figure 1 Japanese quail microsatellite linkage map. The genetic linkage map based on an LOD score threshold of 3 is shown with the estimated Kosambi map distances in cM on the left. Loci on the framework are supported by odds >3 and the possible locations of loci not supported are indicated by an error bar. The autosomal linkage groups are presented as sex-averaged maps while the male-specific map is given for the Z-linkage group. Linkage groups that were assigned to chromosomes through comparative mapping with chicken are designated by CJA followed by a number corresponding to the chicken chromosomes on which they were comparatively mapped. Cross-species markers that were used to assign linkage groups to chromosomes through comparative mapping with chicken are shown in boldface type.

be assigned to these chromosomes in quail (Table 1). It is of interest to note that the microsatellite marker GUJ0001 was mapped to within 2.0 cM of the growth hormone (GH) locus on the East Lansing linkage group E59 and could thus be a useful marker for this gene.

The assignment of the quail linkage groups to chromosomes through comparative mapping with chicken is supported by cytogenetic evidence of high quail–chicken chromosome correspondences. Recent cytogenetic studies based on banding patterns or chromosome painting using fluorescent *in situ* hybridization (FISH) have revealed highly conserved chromosome homology between chicken and quail, with only a few chromosome rearrangements (essentially pericentric inversions) observed in chromosomes 1, 2, 4 and 8 (Schmid *et al.* 2000; Shibusawa *et al.* 2001). In these studies, evidence of conserved synteny between chicken and quail was confirmed not only on the macrochromosomes but also on the microchromosomes as well. On the basis of such highly conserved syntenies, we considered it appropriate to assign quail linkage groups to chromosomes

based on comparative mapping with chicken that utilized one or two orthologous cross-species markers per linkage group. However, because these assignments are based solely on assumptions of homology between markers and between chromosomes, they should be regarded as provisional.

Comparative mapping has proved to be a powerful tool for producing consensus genetic maps within- and between-species (Groenen *et al.* 2000; Kurar *et al.* 2002), verification of quantitative trait loci (Sonstegard *et al.* 2000), identification of candidate genes for quantitative and complex traits (Cox *et al.* 2002) and for studying genome evolution (Burt *et al.* 1999). In this perspective, orthologous cross-species markers serve as useful tools providing anchor points for comparisons across different species. However, the markers used in building this map are anonymous or type II markers (O'Brien 1991), and so to improve comparative mapping with the map-rich species, especially the chicken and human, it would be necessary to place a number of type I markers (genetic markers within or adjacent to known genes) on the map.

The map coverage within the 13 linkage groups is 576 cM. Assuming 50 cM for each of the 14 independent markers, the total map distance would be 1276 cM ($576 + 50 \times 14$), covering about a third of the quail genome of 3800 cM, estimated by comparison with chicken. Therefore, many more microsatellites are needed to obtain a better genome coverage. It has been estimated that about 200 markers evenly spaced at 20 cM or less would be required to achieve a complete genome coverage suitable for full genome scanning projects (Groenen *et al.* 1998).

This map is the first microsatellite linkage map of the Japanese quail and is thus a major step towards the development of a quality molecular genetic map for this species. Recently, the first genetic map for quail was produced exclusively with AFLP markers (Rousset *et al.* 2003). Hence, it would be beneficial in the future to integrate the microsatellite and the AFLP maps in order to provide a powerful tool for the ongoing search for quantitative trait loci controlling egg production and fear-related behavioural traits in quail.

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