IJAS Iranian Journal of Applied Animal Science

Gene Dropping Analysis of Founder Contributions and Allelic Diversity in an under Selected Population of Japanese Quails

Research Article

M. Khaldari[1*] and H. Ghiasi[2]

[1] Department of Animal Science, Faculty of Agriculture, Lorestan University, Khorram-Abad, Iran
[2] Department of Animal Science, Faculty of Agricultural Science, Payame Noor University, Tehran, Iran

Received on: 10 Aug 2016
Revised on: 19 Apr 2017
Accepted on: 30 Apr 2017
Online Published on: Mar 2018

*Correspondence E-mail: khaldari.m@lu.ac.ir

Online version is available on: www.ijas.ir

ABSTRACT

The current study was conducted to consider how pedigree and the gene-dropping analysis can use to monitor genetic diversity, and to recommend a breeding strategy for improving breast weight (BRW) in a population of Japanese quail. A total of 312 birds were divided equally into two lines. One line (S1) was selected for four-week body weight (BW) based on breeding value, and the other (S2) was selected for four-week BRW based on between-family selection. The distributions of allele frequencies originating from the founders were estimated using gene-dropping simulation software for the actual pedigree of each line. The results revealed that the total net genetic improvements in BW and BRW in the S1 and S2 lines were 28.3 and 9.7 g *vs*. 23.3 and 6.8 g, respectively. The average numbers of surviving alleles in the descendants were 59.6 and 31.2 for the S1 and S2 lines, respectively, which were 19.1% and 10% of the total number of assigned alleles in the base population. It can be concluded that for stabilizing the response to selection for improving BRW, it is recommended to use indirect selection of BW based on breeding values. The results obtained from the gene-dropping experiment showed that the between-family selection method results neither in more genetic gain nor in greater remaining genetic variation.

KEY WORDS founder, gene dropping, genetic diversity, Japanese quail.

INTRODUCTION

Over the past decade, substantial progress has been made in genetic selection and the conservation of genetic resources. Genetic selection and the standardization of animal populations to meet various demands depend on effective access to, and the ability to use, genetic diversity. With the increasing ability to change the genetic composition of livestock populations, the conservation of these genetic resources becomes more critical (Blackburn, 2012). However, there has been no experimental evidence demonstrating an exhaustion of genetic variability through a selection plateau (Carlborg *et al*. 2006). Genetic variability (variation) is associated with the additive genetic variance found within a breed (Blackburn, 2012), whereas genetic diversity is defined as the sum of genetic differences in multiple loci among individuals in a population, and is reflected in the phenotypic variation seen in many populations (Man *et al*. 2007). Loss of genetic diversity is often associated with inbreeding and a reduction in reproductive fitness (Frankham *et al*. 2002). Hence, determination of genetic diversity is important in farm animals breeding (Javanmard *et al*. 2008; Mohammadabadi *et al*. 2010; Ruzina *et al*. 2010). In domestic animals, pedigree analysis is a valuable tool for quantifying genetic effects and the loss of genetic variation (Sölkner *et al*. 1998). A large number of studies in horses (Yamashita *et al*. 2010) and cattle (Solkner *et al*. 1998; Melka *et al*. 2012) have used pedigree information

for such analyses. From pedigree information, the level of inbreeding and the relationships among the population can be estimated, as well as the effective population size (N_e), which is regarded as a good indicator of the change in genetic diversity over a long period of time (Boichard *et al*. 1997). N_e is an estimate of the number of animals that would produce the observed rate of inbreeding in the current generation under ideal conditions (Lacy, 1995). One of the primary goals in the management of animal populations is to maintain their genetic diversity at a high level and their inbreeding at a low level (Fernández *et al*. 2005). In addition, genetic diversity can be evaluated by an effective and well-known method called gene-dropping (Yamashita *et al*. 2010). Due to the fact that the mean distribution of allele frequency for a founder should coincide with the genetic contribution computed from a pedigree analysis, the probability of allele extinction can be obtained only through gene-dropping simulations (Honda *et al*. 2002).

Gene-dropping is a simulation procedure in which two unique alleles are assigned to each founder, and the genotypes of all descendants along the actual pedigree are generated following Mendelian segregation rules (MacCluer *et al*. 1986). However, application of this method rests on certain assumptions, such as 50:50 transmission probabilities, no mutation, and no migration. Also, the method is flexible enough to extend for several loci, thus measuring the change in linkage disequilibrium (Baes and Reinsch, 2008). This allows simulating a genome for each animal, in which the number of repetitions refers to the number of unlinked loci (Suwanlee *et al*. 2007). This technique provides considerably more information about population structure than is available from calculations of the proportionate contributions of the founders (MacCluer *et al*. 1986). Although Japanese quail in Iran have been studied by molecular techniques for different purpose (Sohrabi *et al*. 2012; Moradian *et al*. 2014; Ori *et al*. 2014; Moradian *et al*. 2015), but until now researchers have not determined how pedigree and the gene-dropping analysis can be used to monitor genetic diversity, and there is no any recommendation of breeding strategy for improving breast weight (BRW). Hence, the main objective of this study was to examine the efficiency of the selection and to suggest the breeding strategy for improving the BRW in quail. We considered how pedigree analysis and the gene-dropping method can be used to monitor genetic variation, and to help to decide the proper method of selection for increasing the desired trait.

MATERIALS AND METHODS

The experimental Japanese quail population (*Coturnixcoturnix*) originated from a commercial farm in Iran.

To establish the selected lines, a total of 312 birds (generation 0) were randomly selected from the base population and divided equally into two lines. One line (S1 line) was selected to increase body weight (BW) and the other was selected to increase BRW (S2 line). The population had not been selected for any traits before the start of the experiment. The birds in both lines were individually leg-tagged. Two females were placed in two-floor cages and one male mated with them every second day (1:2 male:female). The birds were kept under conditions as presented by Khaldari *et al*. (2010). The eggs were collected daily and labeled by dam number to constitute pedigree. At the time of hatching, the quails were leg-tagged with a numbered plastic plate that was pitched by nip, and quails from each line were placed into separate pens. Two hatches per each generation (four generations total) were performed.

BW was measured at 4 weeks of age in each line. Then, after 2 h without food, all of the birds from hatch 1 in the S2 line were slaughtered, plucked, and eviscerated, and the carcasses were kept for 4 h at 4 ˚C. Each carcass was then weighed without the feet (empty carcass weight). The breasts and legs were separated and the residual was calculated as the back. A total of 80 birds from hatch 1 in the S1 line also were randomly selected and slaughtered to obtain the BRW. BW and BRW were recorded for each line to calculate the direct and correlated responses to selection.

BW at 4 weeks was analyzed with an animal model to predict the breeding values of birds in the S1 line using ASREML software (Gilmour *et al*. 2000), and the superior birds (104 females and 52 males) were selected as the parents of the next generation. The parents in the S2 line, however, were selected for BRW using the between-family selection approach in each generation, all of the birds of hatch 1 were slaughtered, then the birds from the 50% of full-sibling families with the highest family BRW in hatch 1 were used as the parents from hatch 2. The numbers of male and female birds, and the contributing founders in each generation, are presented in Table 1.

The gene-dropping simulation is illustrated in Figure 1, in which the process of one simulation trial is presented with a simple pedigree. To obtain a reliable distribution of allele frequencies in the reference population, the process was replicated 1000 times using Mendel software (Lange *et al*. 2001).

The probability of extinction of alleles originating from a founder, Pr(lost), was calculated from the proportion of replicates in which both alleles derived from the founder did not segregate in the reference population (generation 4). Similarly, the probability of alleles being at a high risk of extinction, Pr(risk), was obtained by the proportion of replicates in which allele frequency (q) was within the range of $0 < q < 0.01$.

Table 1 The number of male and female birds, total and contributing founders in each generation, for 4wk body weight (S1) and 4wk breast weight (S2) lines

Generation	S1 line				S2 line			
	Male	Female	Total founder	Contributed founder	Male	Female	Total founder	Contributed founder
0	52	104	156	156	52	104	156	156
1	196	214	-	113	177	156	-	108
2	202	205	-	94	158	176	-	84
3	204	206	-	69	168	155	-	59
4	169	156	-	64	68	77	-	38

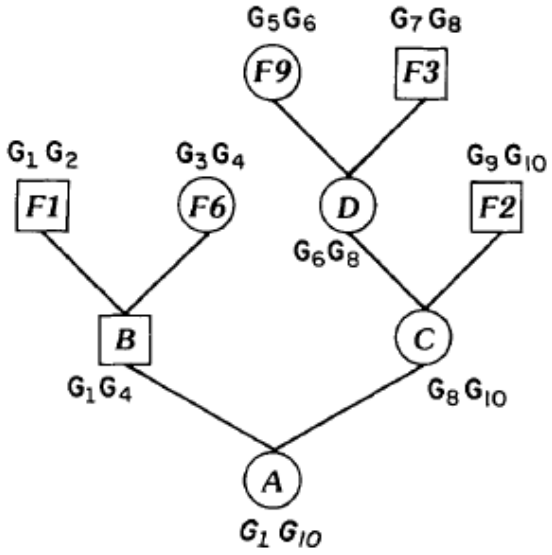

Figure 1 Illustration of gene dropping simulation
Allocation of unique hypothetical alleles (G) for founders (F) and genotype assign to descendants (A, B, C and D) by Mendelian segregation of founder alleles

The upper limit (0.01) of the range was chosen as described by MacCluer *et al.* (1986). Finally, the probability of alleles surviving at a critically low frequency, conditional upon the founder alleles being retained in the reference population, was computed as:

$$\Pr(risk \mid survive) = \frac{\Pr(risk)}{1 - \Pr(lost)}$$

This conditional probability is an indicator of Pr(risk). It should be noted that these three probabilities are conditional on the pedigree structure (Honda *et al.* 2002). The contribution of the founders and the inbreeding coefficients (F) for all animals in the pedigree and F-statistics were calculated using the Eva-Inbred software (Berg, 2010). The F-statistics (F_{IT}, F_{ST}, and F_{IS}) were estimated in each generation to assess the amount of inbreeding and the population structure.

The coefficient F_{IT} is the average inbreeding coefficient, and F_{ST} is the inbreeding coefficient expected under random mating.

The latter was estimated as the average kinship between the sires and dams (parents) of the generation. The third coefficient, F_{IS}, is the deviation from random mating, obtained by the formula of Wright (1969) as:

$$F_{IS} = \frac{F_{IT} - F_{ST}}{1 - F_{ST}}$$

The actual inbreeding (F_{IT}) exceeds the expected level under random mating (F_{ST}) when $F_{IS} > 0$, implying that mating among more closely-related parents than expected is predominant, or that the population is partitioned into subpopulations and mating is more or less restricted within each subpopulation. In contrast, avoidance of inbreeding or mating between subpopulations is predominant in populations with $F_{IS} < 0$.

The effective size of the population was estimated from the increasing rate of F_{ST} per generation (Caballero and Hill, 1992). The generation rate of inbreeding ($\Delta F_{ST, g}$) of F_{ST} was first computed as:

$$\Delta F_{ST, t} = (F_{ST, t} - F_{ST, t-1}) / (1 - F_{ST, t-1})$$

Where:
$F_{ST, t-1}$ and $F_{ST, t}$: coefficients of F_{ST} in two successive generations.

The N_e was then computed as $1 / (2\Delta F_{ST, t})$ (Nomura *et al.* 2001). Finally, we reached the following formula for calculating the average allele frequencies for each founder:

$$f_j = \frac{STA_j}{nR \times 2N} = \sum_{i=1}^{1000} \frac{p_i + q_i}{nR}$$

Where:
STA_j: sum of total alleles.
nR: 1000 is the number of replicates.
N: number of individuals in the last generation.
p_i and q_i: allele frequencies of founder j in the last generation of the i^{th} replication.

RESULTS AND DISCUSSION

The direct and correlated responses to selection for BW and BRW in the S1 and S2 lines are presented in Table 2.

Table 2 Direct and correlated response to selection for body weight (BW) and breast weight (BRW) in S1 and S2 lines (g)

Generation	S1 line		S2 line	
	BW (direct)	BRW (correlate)	BW (correlate)	BRW (direct)
0	-	-	-	-
1	-	-	-	-
2	9.7	2.7	9.2	3.5
3	9.6	2.7	8.9	2.7
4	10.0	4.3	5.2	0.6
Total	28.3	9.7	23.3	6.8

In the current study, the efficacy of the pedigree information and gene-dropping simulation were used in order to conserve the genetic diversity and to suggest a breeding strategy for improving BRW in the long-term response to selection; however, the experiment was a short-term selection. According to Table 2, the direct responses to selection for BW and BRW were 28.3 and 6.8 g in the S1 and S2 lines, respectively. Similarly, the indirect responses to selection for BRW and BW were 9.7 and 23.3 g in the S1 and S2 lines, respectively. The same responses have also been reported by other researchers (Zhao *et al.* 2007; Varkoohi *et al.* 2010). Varkoohi *et al.* (2010) reported a 16.4% correlated response for BW when family selection was directly used for the feed-conversion ratio. Considering the responses to selection in Table 2, the current study does not support using family selection to increase BRW, because the recording of BW is easier and the costs of breeding for BW are lower.

The numbers of birds, inbred birds, F-statistics, and N_e are presented in Tables 3 and 4 for the S1 and S2 lines, respectively. Considering that the efficacy of each breeding program should be assessed at the same level of inbreeding, the results from the pedigree data showed that the estimated generational rate of inbreeding was around 0.004 (0.4%) in the S1 line, but the S2 line had a fluctuation of 0.008 - 0.013 (0.8%1.3%). Changes in inbreeding rates corresponded to changes in N_e (Tables 3 and 4); in other words, increased inbreeding is an outcome of decreased N_e, and *vice versa* (Gutie *et al.* 2008). For monitoring the breeding strategy, N_e is an important key parameter because it is concerned with inbreeding; it affects inbreeding depression and decreases genetic diversity. The N_e for the current population was 45.5 and 61.7 for the S1 and S2 lines, respectively (Tables 3 and 4). Goddard and Smith (1990) proposed the N_e to be at least 40. When N_e is > 100, the response to selection continues linearly with the selection program. This is clear in broilers, whose growth heritability has remained at approximately 0.3 after 50 years of extreme selection (Hill, 2000). Frankham *et al.* (2002) also reported that N_e of 50 is required to withstand the effects of inbreeding, whereas a size of 500 is essential to sustain the genetic diversity and evolutionary potential of the population for several generations (Frankham *et al.* 2002).

Meuwissen (2009) also argued that N_e of at least 50 is adequate, although 100 is recommended. In this study, N_e did not go below the critical value, but a small N_e and an increasing inbreeding coefficient will lead to lower genetic diversity in the future, especially in the S2 line, as Melka *et al.* (2012) warned with regard to dairy cattle. Therefore, two points about family selection are understood. One is that inbreeding and then N_e have a fluctuation in two successive generations (Table 4) and the other is that founders make more balanced genetic contributions to the last generation due to the low variance of family size. However, for evaluating the retained genetic diversity in the lines under selection, the results of gene-dropping are more acceptable. The results revealed that of the156 base founder birds for each line, only 64 in the S1 line (22 males and 42 females) and 38 in the S2 line (24 females and 14 males), contributed their genetic material to the last generation. The average genetic contributions of male and female founders to the last generation in both lines were approximately 1.87% and 1.40%, respectively. In the S1 line, a total of 87% of the last generation's genome was contributed by 34 founders, consisting of 13 males (37%) and 21 females (50%), respectively. Forty-two founders contributed 95% to the total genome, while 22 founders contributed only 5%. Similarly, in the S2 line, 28 and 33 founders contributed 87% and 95% of the total genome, while five founders contributed 5%. Genetic contribution based on pedigree, average allele frequency, probability of being lost, and the risk of future generations of founders with extreme genetic contributions in the S1 and S2 lines are presented in Tables 5 and 6, respectively.

The average number of alleles surviving in each generation are presented in Figure 2. The average numbers of surviving alleles in the last generation of the S1 and S2 lines were 59.6 and 31.2, respectively, or approximately19.1% and 10% of the total number of assigned alleles in the base population.

The results of gene-dropping showed that the genetic contribution of the founders to the last generation in S2 line was more equal than S1 line (Tables 5 and 6). In addition, the average allele frequency over all of the replicates for each founder agreed with the genetic contribution obtained in the pedigree analysis.

Table 3 Number of birds (N), inbred birds, F-statistics and effective population size (Ne) in each generation at S1 line

Generation	N	N. Inbred	F_{IT}	F_{ST}	F_{IS}	ΔF	Ne
0	156	0	0	0	0	0	-
1	410	0	0	0	0	0	-
2	407	14	0.0086	0.0033	0.0053	0.0033	151.5
3	410	67	0.0152	0.0109	0.0044	0.0076	65.8
4	325	116	0.0168	0.0218	-0.0051	0.011	45.5
Total	1708	197	0.0088	-	-	-	-

ΔF: rate of inbreeding and Ne: effective size.

Table 4 Number of birds (N), inbred birds, F-statistics and effective population size (Ne) in each generation at S2 line

Generation	N	N. Inbred	F_{IT}	F_{ST}	F_{IS}	ΔF	Ne
0	156	0	0	0	0	0	-
1	333	0	0	0	0	0	-
2	334	0	0.0086	0.0033	-0.0023	0.0033	151.5
3	323	33	0.0167	0.0162	0.0004	0.0165	30.3
4	145	30	0.0158	0.0241	-0.0085	0.0081	61.7
Total	1291	63	0.0064	-	-	-	-

ΔF: rate of inbreeding and Ne: effective size.

From the distributions, much information was derived for the management of genetic diversity, such as Pr(lost), the probability of alleles surviving at a critically low frequency, and Pr(risk). The results showed that the founders with higher genetic contributions had lower Pr(lost), and Pr(lost) increased as the genetic contribution decreased (Tables 5 and 6). For the management of genetic diversity, Pr(lost) provide suseful information. For example, the low Pr(lost) of the founders implies that alleles can be transmitted to the progeny (Trinderup *et al*. 1999; Yamashita *et al*. 2010; Melka *et al*. 2012). In addition, Pr(lost) for the three founders with the highest genetic contributions in both lines was near zero, but their surviving alleles (Pr(risk|survive)) had a relatively high risk of future extinction (0.28, 0.24, and 0.37 *vs*. 0.04, 0.10, and 0.08 in the S1 and S2 lines, respectively) (Tables 5 and 6). In contrast, the Pr(lost) for the three founders with the lowest contribution was high (>0.75), while their surviving alleles had a relatively low Pr(risk). The high Pr(lost) and the low Pr(risk|survive) of alleles indicate that the alleles passed from a strong drift in the early generations. On the other hand, the lower probability of genome loss (for founders 147, 187, and 148 of the S1 line and 62, 85, and 114 of the S2 line) reflects that their alleles had a higher chance of being transmitted to the reference population. In contrast, the low Pr(lost) and the relatively high Pr(risk) means that the genetic contributions of the founders were not fully informative for the distribution of allele frequency. This is in agreement with the results of Honda *et al*. (2002) and Yamashita *et al*. (2010). From the gene-dropping results, it was also evident by comparing two founders from S1 line (263 and 505), in whom Pr(lost)=0 and Pr(risk) was the same, that the genetic contribution of the former was approximately 2.5 times higher than that of the latter (Table 5). The same status was noted for founders 63 and 422 of the S2 line (Table 6).

Nevertheless, all founders had a significant probability of future extinction. Although the genetic contributions of some founders to the reference populations were low, several founders (for example, founder 231 of the S1 line) showed low Pr(lost), which implies that a partial proportion of the reference population was connected to these founders without severe bottle necking. These results are in agreement with what other researchers have reported (Honda *et al*. 2002; Yamashita *et al*. 2010; Melka *et al*. 2012). Therefore, it seems that the gene-dropping method gives more useful information than a pedigree analysis. In addition, the gene pools of the last generations of the S1 and S2 lines were formed by only 64 and 38 of the 156 primary founders, respectively. This indicates that the major cause of loss of diversity is random genetic drift, which is in agreement with Melka *et al*. (2012). This is also clear from the allelic diversity parameter. The number of surviving alleles is a measure of genetic diversity relative to the base population, which is called allelic diversity (Yamashita *et al*. 2010; Caballero and García-Dorado, 2013). The average surviving numbers of alleles were 59.6 and 31.2 in the last generation in the S1 and S2 lines, respectively, or approximately 19.1% and 10% of the total number of assigned alleles (312) in the base population. According to Figure 2, there was a severe decline of surviving alleles for the S2 line during the two first generations, before a plateau between generations 3 and 4. The decrease for the S1 line was low, and the final decline agreed with the period of intensive use of a limited number of founders for breeding. These results strongly suggest that genetic diversity has decreased in the S2 line after three useful generations of selection. In general, heterozygosity and allelic diversity are two of the most important measures of genetic diversity in animal genetic resources. Allelic diversity refers to the average number of alleles at each locus.

Table 5 A more detailed description of allele frequency and extinction risk for founders contributing to the last generation in S1 line

ID	Sex	Genetic contribution	Allele frequency		Pr(lost)	Pr(risk)	Pr(risk|survive)
			Average	CV (%)			
263	M	0.0577	0.0568	54.5	0.0000	0.2818	0.2818
513	F	0.0435	0.0441	62.4	0.0061	0.2455	0.2476
186	M	0.0400	0.0397	67.2	0.0061	0.3697	0.3720
220	F	0.0398	0.0419	69.9	0.0242	0.3091	0.3168
219	M	0.0398	0.0387	71.3	0.0242	0.3515	0.3602
.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.
505	F	0.0223	0.0223	58.1	0.0000	0.2727	0.2727
.		.	.	.	.	.	.
.		.	.	.	.	.	.
231	M	0.0015	0.0015	48	0.5636	0.1152	0.2639
147	F	0.0012	0.0008	39.4	0.7697	0.0545	0.2368
187	F	0.0012	0.0013	32.4	0.7576	0.0545	0.2250
148	M	0.0012	0.0012	45.2	0.7758	0.0485	0.2162

ID: identification; M: male; F: female; Pr(lost): probability of allele extinction; Pr(risk): probability of alleles being at high risk of extinction and Pr(risk|survive): probability of alleles surviving at critically low frequency.
CV: coefficient of variation.

Table 6 A more detailed description of allele frequency and extinction risk for founders contributing to the last generation in S2 line

ID	Sex	Genetic contribution	Allele frequency		Pr(lost)	Pr(risk)	Pr(risk|survive)
			Average	CV (%)			
467	F	0.0534	0.0559	58.7	0.0000	0.0467	0.0467
63	M	0.0474	0.0465	85.1	0.0400	0.1000	0.1042
424	M	0.0466	0.0429	60.9	0.0133	0.0800	0.0811
64	F	0.0457	0.0424	70.8	0.1067	0.0600	0.0672
102	M	0.0422	0.0473	62.6	0.0600	0.0467	0.0496
101	.	.	.	.	.	.	.
374	.	.	.	.	.	.	.
422	M	0.0198	0.0190	54.1	0.0467	0.1267	0.1329
.		.	.	.	.	.	.
103		.	.	.	.	.	.
113	F	0.0022	0.0025	41.2	0.7200	0.0533	0.1905
114	M	0.0022	0.0019	40.2	0.7667	0.0733	0.3143
62	F	0.0017	0.0016	37.5	0.7800	0.0533	0.2424
85	F	0.0013	0.0015	40.7	0.7467	0.0733	0.2895

ID: identification; M: male; F: female; Pr(lost): probability of allele extinction; Pr(risk): probability of alleles being at high risk of extinction and Pr(risk|survive): probability of alleles surviving at critically low frequency.
CV: coefficient of variation.

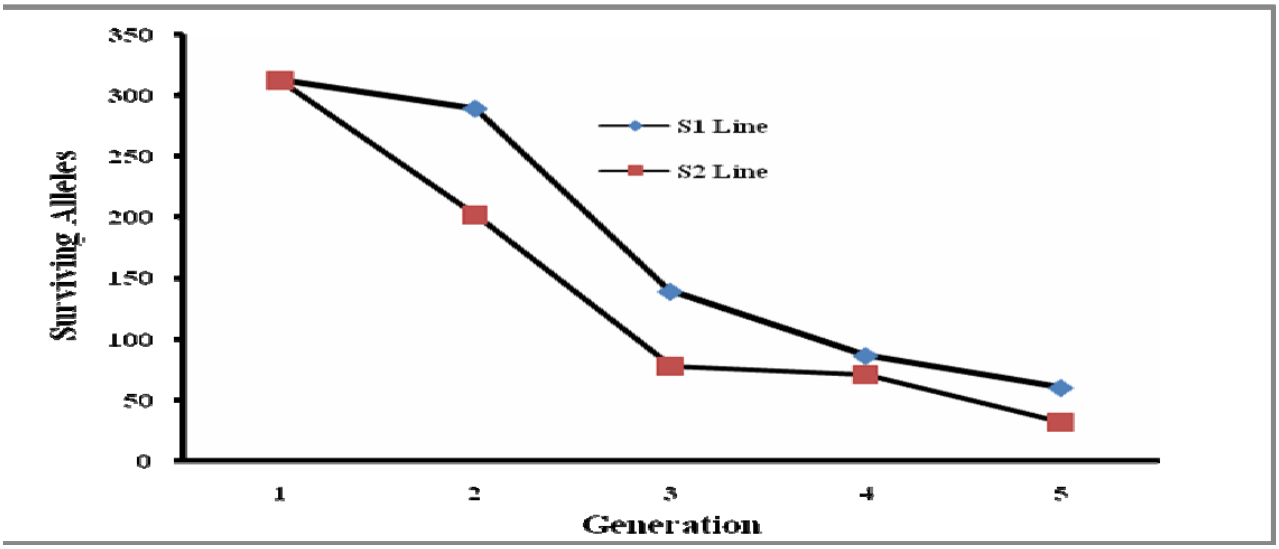

Figure 2 Average number of alleles surviving in each generation of S1 and S2 lines

The loss of heterozygosity is dependent on the rate of inbreeding, which causes an increase of homozygosity and lower fitness, but a lack of allelic diversity prevents long-term response to selection (Falconer *et al*. 1996). Inbreeding is minimized when the contributions of ancestors to the next generation are equal (Sonesson and Meuwissen, 2000; Sorensen *et al*. 2008).

This may be secured by family selection, which uses all of the offspring of a family and thus decreases the family-size variance, as was observed in the present study for the S2 line. However, the intensive use of a limited number of founders or families for breeding (discarding 50% of the family in each generation) greatly decreased the number of surviving alleles and contributing founders in the last generation for S2 compared to S1.

CONCLUSION

It can be concluded that individual selection based on breeding values can be used as a selection criterion to improve the BRW trait because the correlated response to BRW is greater than direct selection (9.7 *vs*. 6.8). This is due to using between- and within-variance of families by individual selection (the S1 line) relative to between-family selection with only between-family variance (the S2 line). From this point of view, individual selection is recommended to improve growth and BRW traits. At the level of retained genetic diversity as well, it is suggested to use individual selection to increase BRW. Therefore, gene-dropping is a valuable tool in optimizing decisions to preserve genetic variability, and it is more useful than pedigree analysis.

ACKNOWLEDGEMENT

The authors are very thankful of research affairs of the Lorestan university to support the funds of this study.

REFERENCES

Baes C. and Reinsch N. (2008). TIGER: A software system for fine-mapping quantitative trait loci. *Arch. Tierzucht*. **51(4),** 402-412.

Blackburn H. (2012). Genetic selection and conservation of genetic diversity. *Reprod. Domest. Anim*. **47(4),** 249-254.

Berg P. (2010). EVA version 1.3. http://eva.agrsci.dk. Accessed Mar. 2013.

Boichard D., Maignel L. and Verrier E. (1997). The value of using probabilities of gene origin to measure genetic variability in a population. *Genet. Sel. Evol*. **29,** 5-23.

Caballero A. and García-Dorado A. (2013). Allelic diversity and its implications for the rate of adaptation. *Genetics*. **195(4),** 1373-1384.

Caballero A. and Hill W. (1992). Effective size of nonrandom mating populations. *Genetics*. **130(4),** 909-916.

Carlborg Ö., Jacobsson L., Åhgren P., Siegel P. and Andersson L. (2006). Epistasis and the release of genetic variation during long-term selection. *Nat. Genet*. **38,** 418-420.

Falconer D.S., Mackay T.F. and Frankham R. (1996). Introduction to Quantitative Genetics. Benjamin Cummings, Wilmington, Delaware, USA.

Fernández J., Villanueva B., Pong-Wong R. and Toro M.A. (2005). Efficiency of the use of pedigree and molecular marker information in conservation programs. *Genetics*. **170(3),** 1313-1321.

Frankham R., Ballou G.D. and Briscoe D.A. (2002). Introduction to conservation genetics. Cambridge University Press. Cambridge, United Kingdom.

Gilmour A.R., Cullis B.R., Welham S.J. and Thompson R. (2000). ASReml Users' Manual. New South Wales Agriculture, Orange, Australia.

Goddard M. and Smith C. (1990). Optimum number of bull sires in dairy cattle breeding. *J. Dairy Sci*. **73(4),** 1113-1122.

Gutié J.P., Cervantes I., Molina A., Valera M. and Goyache F. (2008). Individual increase in inbreeding allows estimating effective sizes from pedigrees. *Genet. Sel. Evol*. **40(4),** 359-378.

Hill W.G. (2000). Maintenance of quantitative genetic variation in animal breeding programmes. *Livest. Prod. Sci*. **63(2),** 99-109.

Honda T., Nomura T., Fukushima M. and Mukai F. (2002). Gene dropping analysis of founder contributions in a closed Japanese black cattle population. *Anim. Sci. J*. **73(2),** 105-111.

Javanmard A., Mohammadabadi M.R., Zarrigabayi G.E., Gharahedaghi A.A., Nassiry M.R., Javadmansh A. and Asadzadeh N. (2008). Polymorphism within the intron region of the bovine leptin gene in Iranian Sarabi cattle (*Iranian Bos taurus*). *Russian J. Genet*. **44(4),** 495-497.

Khaldari M., Pakdel A., Mehrabani Yegane H., Nejati Javaremi A. and Berg P. (2010). Response to selection and genetic parameters of body and carcass weights in Japanese quail selected for 4-week body weight. *Poult. Sci*. **89(9),** 1834-1841.

Lacy R.C. (1995). Clarification of genetic terms and their use in the management of captive populations. *Zoo Biol*. **14(6),** 565-577.

Lange K., Cantor R., Horvath S., Perola M., Sabatti C., Sinsheimer J. and Sobel E. (2001). Mendel version 4.0: a complete package for the exact genetic analysis of discrete traits in pedigree and population data sets. *Am. J. Hum. Genet*. **69(1),** 1886.

MacCluer J.W., VandeBerg J.L., Read B. and Ryder O.A. (1986). Pedigree analysis by computer simulation. *Zoo Biol*. **5(2),** 147-160.

Man W., Nicholas F. and James J. (2007). A pedigree-analysis approach to the descriptive epidemiology of autosomal-recessive disorders. *Prev. Vet. Med*. **78(3),** 262-273.

Melka M., Sargolzaei M., Miglior F. and Schenkel F. (2012). Genetic diversity of Guernsey population using pedigree data and gene-dropping simulations. *Animal*. **7(2),** 192-201.

Meuwissen T. (2009). Genetic management of small populations: A review. *Acta. Agric. Scandinavica*. **59(2),** 71-79.

Mohammadabadi M.R., Nikbakhti M., Mirzaee H.R., Shandi A., Saghi D.A., Romanov M.N. and Moiseyeva I.G. (2010). Genetic variability in three native Iranian chicken populations of the Khorasan province based on microsatellite markers. *Russian J. Genet*. **46(4),** 505-509.

Moradian H., Esmailizadeh A.K., Sohrabi S. and Mohammadabadi M.R. (2015). Identification of quantitative trait loci associated with weight and percentage of internal organs on chromosome 1 in Japanese quail. *J. Agric. Biotechnol*. **6(4),** 143-158.

Moradian H., Esmailizadeh A.K., Sohrabi S.S., Nasirifar E., Askari N., Mohammadabadi M.R. and Baghizadeh A. (2014). Genetic analysis of an F2 intercross between two strains of Japanese quail provided evidence for quantitative trait loci affecting carcass composition and internal organs. *Mol. Biol. Rep*. **41(7),** 4455-4462.

Nomura T., Honda T. and Mukai F. (2001). Inbreeding and effective population size of Japanese Black cattle. *J. Anim. Sci*. **79(2),** 366-370.

Ori R.J., Esmailizadeh A.K., Charati H., Mohammadabadi M.R. and Sohrabi S.S. (2014). Identification of QTL for live weight and growth rate using DNA markers on chromosome 3 in an F2 population of Japanese quail. *Mol. Biol. Rep*. **41(2),** 1049-1057.

Ruzina M.N., Shtyfurko T.A., Mohammadabadi M.R., Gendzhieva O.B., Tsedev T. and Sulimova G.E. (2010). Polymorphism of the *BoLA-DRB3* gene in the Mongolian, Kalmyk, and Yakut cattle breeds. *Russian J. Genet*. **46(4),** 456-463.

Sohrabi S.S., Esmailizadeh A.K., Baghizadeh A., Moradian H., Mohammadabadi M.R., Askari N. and Nasirifar E. (2012). Quantitative trait loci underlying hatching weight and growth traits in an F2 intercross between two strains of Japanese quail. *Anim. Prod. Sci*. **52(11),** 1012-1018.

Sölkner J., Filipcic L. and Hampshire N. (1998). Genetic variability of populations and similarity of subpopulations in Austrian cattle breeds determined by analysis of pedigrees. *Anim. Sci*. **67(2),** 249-256.

Sonesson A.K. and Meuwissen T.H.E. (2000). Maring schemes for optimum contribution selection with constrained rates of inbreeding. *Genet. Sel. Evol*. **32(3),** 231-238.

Sørensen M.K., Sørensen A.C., Baumung R., Borchersen S. and Berg P. (2008). Optimal genetic contribution selection in Danish Holstein depends on pedigree quality. *Livest. Sci*. **118(3),** 212-222.

Suwanlee S., Baumung R., Sölkner J. and Curik I. (2007). Evaluation of ancestral inbreeding coefficients: Ballou's formula versus gene dropping. *Conserv. Genet*. **8(2),** 489-495.

Trinderup M., Jorgensen J.N. and Hansen M. (1999). Conservation considerations on Danish Shorthorn cattle using pedigree analysis. *Anim. Gen. Res. Inf*. **26,** 27-33.

Varkoohi S., Babak M.M.S., Pakdel A., Javaremi A.N., Zaghari M. and Kause A. (2010). Response to selection for feed conversion ratio in Japanese quail. *Poult. Sci*. **89(8),** 1590-1598.

Wright S. (1969). The Theory of Gene Frequencies. The University of Chicago Press, Chicago, USA.

Yamashita J., Hironori O., Hasegawa T., Honda T. and Nomura T. (2010). Gene dropping analysis of ancestral contributions and allele survival in Japanese thoroughbred population. *J. Equin Sci*. **21(3),** 39-45.

Zhao G., Chen J., Zheng M., Wen J. and Zhang Y. (2007). Correlated responses to selection for increased intramuscular fat in a Chinese quality chicken line. *Poult. Sci*. **86(11),** 2309-2314.