Long Term Selection for Small Body Weight in Japanese Quail I : Direct Selection Response from 60 to 65th Generations

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It is important to know the limit of artificial selection for efficient animal production. The aim of this research was to examine whether the selection for small body weight in Japanese quail has reached to the limit after the long term selection over 65 generations. In this research, two lines, SS and RR were compared. RR line was produced by random mating in a closed population as the control, and SS line was selected for small body weight at 6 weeks of age until 65 generations. Additionally, the data of LL line selected for large body weight was used to evaluate a selection limit in SS line though the details were not shown. Each line was composed of about 30 pair-matings, and body weight measurement was performed every week until 6 weeks of age, but the body weights of candidate birds selected for production of next generation were measured until 15 weeks of age. In the first step of selection, 4 males and 4 females were selected as a general rule among the offspring from each pair-mating at about 4 weeks of age. In the second step of selection, one male and one female were chosen by body weight at 6 weeks of age from 8 individuals selected in the first step, and 30 pair-matings were arranged with the individuals having no consanguineous relation in the preceding 4 generations. Mean body weight of SS line during 60-65 generations was 59.5g and that of RR line was 106.5 g, and the difference was significant ($P < 0.01$). Selection pressure (SP) in the two lines was constant throughout the generations. Selection intensity (SI) in SS line was in the negative direction, and that in RR line was near zero. Estimated heritability in the two lines was variable from generation to generation. Realized heritabilities in SS line increased in both males and females during two terms of 54 to 59 and 60 to 65 generations. The selection response increased in the negative direction in response to cumulative selection differential. The observed ratio of mean body weight at 6 weeks of age in SS line to that in LL line (ORM) and observed ratio of difference between mean body weight at the same age in SS line and that in LL line to the standard deviation of body weight in RR line (OR) suggested that selection limit may not have been reached in SS line after the long term selection for 65 generations and it may be possible to expect further genetic improvement.

Generally, artificial selection during a very long period would reach to a limit on account of decrease in genetic diversity. However, selection in the direction for small

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body weight was found to show the different tendency from the selection for large body weight. Miniaturization of body size is an interesting biological phenomenon from the evolutionary point of view. The SS line established in the present study would be useful for the research from molecular biologic and metabolic aspects to have an insight into evolutionary mechanism of miniaturization.

Key word : selection limit, body weight, small size, heritability, Japanese quail

Introduction

Selection response is generally represented as an important genetic parameter to improve the economic traits and produce desirable traits in the domestic animals. Because the relationships among traits are divergent : direct or indirect and genetic or non-genetic, the balance between them needs to be taken into account in a selection experiment (Peebles and Marks, 1991a). However, the selection response tends to decrease and eventually disappear in the long term selection applied to a closed population because of increase in homozygosity or genetic drift due to inbreeding (Boesger *et al.*, 1975 ; Hanvenstein *et al.*, 1988 ; Leitch *et al.*, 1994). In poultry, an inbreeding causes several obstructions in reproductive functions ; a decline in the rate of egg-laying, fertilization, hatching, raising and survival (Nestor and Bacon, 1982 ; Nestor *et al.*, 1996). It is necessary to achieve the selection limit without depression of reproductive ability due to inbreeding (Meuwissen and Sonesson, 1998). Heterosis effect in the crosses between divergently selected lines would be an example to support such breeding strategy (Moritsu *et al.*, 1997). Selection efficiency to achieve the limit for one trait is different depending on animal species, sexes, selection methods and environmental effects. It is basically related to a size of a population, degree of inbreeding, magnitude of genetic variation and additive effects of genes related to a trait selected (Anthony *et al.*, 1990 ; Lofgren and Stewart, 1994 ; Marks *et al.*, 1990 ; Oikawa *et al.*, 2000). As indirect response in the selection experiment for growth, environmental influences are important (Takahashi *et al.*, 1984 ; Windon, 1990 ; Marks, 1991a ; Marks, 1991b ; Peebles and Marks, 1991b ; Kadarmideen *et al.*, 2000). Furthermore, the selection response might be different between males and females (Bihan-duval *et al.*, 1998 ; Yang *et al.*, 1998). Ely *et al.* (1998) have reported the difference in mortality between sexes, which was inferred to be caused by the differences in physiological characteristics.

In the present research, we performed a selection experiment with Japanese quail through 65 generations in which inbreeding was avoided to keep normal reproductive ability, and investigated whether phenotypic response to the selection for small body weight reached to the limit.

Materials and Methods

Animals

A divergent selection by body weight at 6 weeks of age was performed in Japanese

quail for a long term of 65 generations in Laboratory of Animal Production, Faculty of Agriculture, Saga University. Following 3 lines were established : SS and LL lines were selected for small and large body weight, respectively, whereas RR line was produced by random mating in a closed population as a control. In this research, the two lines, SS and RR lines were compared. Additionally, the data of LL line were used as a reference to evaluate selection limit, though the details were not shown in this report.

Body weight measurement was carried out for all birds every week until 6 weeks of age, but the birds selected for production of next generation were measured until 15 weeks of age.

Selection and Mating Methods

The three lines, SS, RR and LL lines, were composed of about 30 pair-matings, and selection was performed in the two steps in each generation. In the first step of selection, 4 male and 4 female offspring from each pair-mating were selected as a general rule at about 4 weeks of age, and, in the second step of selection, one male and one female were selected to produce the next generation by body weight at 6 weeks of age toward the smaller direction in SS line and the larger direction in LL line. RR line was similarly maintained by random selection as the control. All pairs were arranged with the individuals having no blood relations in the 4 preceding generations to avoid a mating of close relatives and maintained until the end of mating period without exchanging a pair-mate.

Management (Hatching and Raising Condition)

The eggs for hatching were collected after the 4th day of initial mating, stored in a refrigerator kept at about 13°C and transferred every 10 days into an incubator which was kept at 37.7°C and 70% humidity. At the 6th day of incubation, all eggs were examined by candling. The eggs judged as infertile or having dead embryos were removed, and the contents were checked. The eggs that did not hatch were examined for the stages of embryonic death at the 20th day in SS line and at 19th day in RR line.

All hatched chicks were raised in the electric brooder until 2 weeks of age and in the herd brooder until 4 weeks of age. Thereafter, they were transferred into the individual cages, and a pair-mating was performed with birds selected in the second step during 6 to 15 weeks of age in the mating cage. The temperature in the electric brooder was kept at 40°C during a few days after hatch, and lowered to 35°C during the rest of first week and 30°C during the second week. The temperature in the room installed with the herd brooder was kept at 28°C during the third week and at the range of 15–30°C after the fourth week. Lighting time was 24 hours until the second week, and then light period was gradually reduced in the third week ; 21 hours in the first and second days and 20 hours in the third day. Thereafter, the lightening condition was fixed at 14 hours light and 10 hours dark.

All quail were fed on the diet for laying quail (24% crude protein, 2,710kcal) supplemented with fish meal containing 60% crude protein. Total crude protein content in the diet was adjusted at 28%. The diet and water were given continuously.

Calculation of Statistical and Genetic Parameters

To estimate distribution pattern of body weight at the age of 6 weeks, both

skewness and kurtosis were calculated. Selection pressure (SP) was given as the ratio of the number of birds selected for production of next generation (SB) to a whole parental population (Pop) in each line and generation. Selection intensity (SI) was shown as a ratio of the selection differential to the standard deviation of body weight at 6 weeks of age in each line and generation. Estimated heritabilities of body weight at each generation were shown by regression of offspring on mid-parental values at 6 weeks of age in SS and RR lines (Hill and Thompson, 1977). Realized heritabilities at each generation in SS line were calculated by dividing selection response (genetic gain) with cumulative selection differential through generations. To characterize selection response, an estimation method of selection limit suggested by Falconer and Mackey (1996) was used. The observed ratio of mean body weight at 6 weeks of age in SS line to that in LL line was given as ORM values, and the ratio of observed range (OR) was calculated by dividing the difference between mean body weight at 6 weeks of age in SS line and that in LL line by standard deviation of body weight at the same age in RR line.

Results

Selection Pressure and Selection Intensity

Table 1 shows the progress of selection during 60–65 generations in SS and RR lines. The average numbers of birds examined per generation (Pop) were 193.6 and 206.9 in SS line and RR line, respectively. Number of selected birds (SB) in SS and RR lines ranged from 56 to 70 and from 52 to 64, respectively, and the mean was 62.8 in SS line and 60.3 in RR line. Selection pressure (SP) in SS line varied widely through the six generations and the mean was 33.5%, whereas SP in RR line was relatively constant and the mean was 29.2%. Selection intensity (SI) in SS line varied from -0.62 to -0.04 , whereas SI in RR line ranged from -0.20 to 0.27 . The means of SI value in SS line and RR line was -0.33 and 0.04 , respectively.

Changes in body weight at 6 weeks of age over generations

Figures 1 and 2 show changes in body weight at 6 weeks of age from 60 to 65 generations in males and females, respectively. Body weight did not change significantly

Table 1. Selection pressure and selection intensity in SS and RR lines

Item	Line	Generations						Mean
		60	61	62	63	64	65	
Pop	SS	229	228	163	163	223	159	193.6
	RR	176	210	250	187	204	218	206.9
SB	SS	58	70	56	66	58	70	62.8
	RR	52	60	60	63	64	64	60.3
SP (%)	SS	25.3	30.7	34.4	40.5	26.0	44.0	33.5
	RR	29.6	28.6	24.0	33.0	31.4	29.4	29.2
SI	SS	-0.62	-0.39	-0.37	-0.45	-0.04	-0.12	-0.33
	RR	-0.20	0.07	0.06	0.04	0.06	0.27	0.04

Pop : Total number of birds examined at each generation, SB : Number of birds selected, SP : Selection pressure, SI : Selection intensity.

Fig. 1. Mean and standard deviation of body weight of males at 6 weeks of age in SS and RR lines at each generation., Number of birds examined is indicated in parenthesis., **The difference between the two lines was significant at 1% level.

Fig. 2. Mean and standard deviation of body weight of females at 6 weeks of age in SS and RR lines at each generation., Number of birds examined is indicated in parenthesis., **The difference between the two lines was significant at 1% level.

over these generations in each line. The differences between SS and RR lines were significant in both males and females ($P < 0.01$) at each generation. The overall difference from 60 to 65 generations was 45.5 ± 1.7 g (Mean $\pm$ standard deviation, $N = 6$) and 57.3 ± 8.0 g ($N = 6$) for males and females, respectively.

Distribution of body weight at 6 weeks of age over generations

Tables 2 and 3 show the results of analysis of variance and fitness test for normal distribution concerning body weight at 6 weeks of age from 60 to 65 generations, respectively. The effect of generation was not significant. The effect of line was highly significant in both males and females ($P < 0.01$). Values of skewness were -0.02 and 0.19 in males of SS and RR lines, respectively. The distributions in males of SS and RR

lines were characterized by wide-based type. However, the variance in SS line was smaller than that in RR line. Skewness value in females of SS and RR lines was 0.18 and 0.20, respectively, showing the same trends as in males. Kurtosis value was 3.18 and 2.77 in males of SS and RR lines, respectively, indicating that the distribution in SS line was narrower than that in RR line. However, the kurtosis values in females of SS and RR lines were 2.82 and 3.50, respectively, indicating that females of RR line showed narrower distribution compared to SS females. Coefficient of variance was 8.1% and 6.5% for males of SS and RR lines, respectively, and 12.0% and 10.0%, respectively, for the females.

Realized and estimated heritability for body weight at 6 weeks of age

Table 4 shows realized heritabilities which were calculated with the data collected during 54–59 generations and 60–65 generations in SS line. Realized heritabilities in the two periods were 0.41 and 0.51 in males and 0.17 and 0.39 in females, respectively. Combining males and females, the mean heritability increased from 0.30 in the former period to 0.46 in the latter period.

Table 2. Analysis of variance of body weight at 6 weeks of age from 60 to 65 generations

Source	Sex	DF	Sum of square	Mean of square	F value
Generation	Male	5	5.9	1.2	0.72
	Female	5	109.6	21.9	0.57
Line	Male	1	6210.8	6210.8	3810.3**
	Female	1	9832.7	9832.7	256.2**
Error	Male	5	8.1	1.6	—
	Female	5	191.3	38.3	—

DF : Degree of freedom, ** It was significant at 1% level.

Table 3. Normality test for frequency distribution of body weight at 6 weeks of age in SS and RR lines

Line	Sex	N	Mean (g)	CV (%)	Skewness	Kurtosis
SS	Male	586	56.7 (4.6)	8.1	−0.02	3.18
	Female	564	62.0 (7.4)	12.0	0.18	2.82
RR	Male	610	101.8 (6.6)	6.5	0.19	2.77
	Female	611	120.4 (12.0)	10.0	0.20	3.50

N : Number of birds examined in 60–65 generations, SD : Standard deviation, CV : Coefficient of variance (%), () : standard deviation of means.

Table 4. Realized heritability for body weight at 6 weeks of age based on the data during 54–59 and 60–65 generations in SS line

Generations	Male	Female	Mean
54–59	0.41 (0.13)	0.17 (0.08)	0.30 (0.12)
60–65	0.51 (0.17)	0.39 (0.19)	0.46 (0.19)

() : Standard error of means.

Table 5 shows heritabilities estimated by regression of offspring on mid-parental values from 60 to 65 generations. In SS line, the estimates were 0.78 and 0.45 in males at the 60th and 65th generation, respectively and tended to decrease with progress of generations, while the estimate was variable in the females during these generations. In RR line, the mean estimate was relatively constant throughout generations.

Selection response of body weight at 6 weeks of age from 60 to 65 generations

Summary of the selection response from 60 to 65 generations is shown in Fig. 3. The mean response of males and females increased in the positive direction temporarily during 60–62 generations, but, thereafter tended to decrease in the intended negative direction.

Selection limit for small body weight

Table 6 shows the indices concerning selection limit for small body weight in this experiment. Observed ratio of means (ORM) tended to decrease slightly in both males and females over the generations. However, absolute values of observed range (OR) were larger in males than in females, and tended to increase in the negative direction in both sexes with generations.

Table 5. Heritability of body weight at 6 weeks of age estimated by regression of offspring on midparental values in SS and RR lines

Line	Sex	Generations					
		60	61	62	63	64	65
SS	Male	0.78(0.16)	0.35(0.11)	0.72(0.26)	0.68(0.15)	0.37(0.08)	0.45(0.11)
	Female	0.49(0.17)	0.47(0.12)	1.27(0.37)	0.81(0.17)	0.25(0.21)	0.68(0.19)
	Mean	0.62(0.16)	0.40(0.11)	0.99(0.31)	0.74(0.16)	0.31(0.14)	0.56(0.15)
RR	Male	0.25(0.17)	0.59(0.17)	0.39(0.11)	0.32(0.14)	0.34(0.20)	0.66(0.18)
	Female	0.61(0.17)	0.74(0.17)	0.45(0.11)	0.52(0.14)	0.34(0.20)	0.66(0.33)
	Mean	0.43(0.17)	0.67(0.19)	0.42(0.10)	0.43(0.16)	0.34(0.20)	0.67(0.25)

() : Standard error of means.

Fig. 3. Selection response of body weight at 6 weeks of age from 60 to 65 generations in SS line., Selection response: the difference between mean body weight of all progeny and that of pre-selected parental population.

Table 6. Indices concerning selection limit for small body weight at 6 weeks of age

Item	Sex	Generations						Mean (SD)
		60	61	62	63	64	65	
ORM	Male	0.27	0.26	0.27	0.27	0.25	0.24	0.26 (0.01)
	Female	0.26	0.25	0.25	0.26	0.24	0.23	0.25 (0.01)
OR	Male	-21.9	-23.3	-22.7	-23.1	-24.2	-24.8	-23.3 (1.04)
	Female	-16.5	-17.2	-17.0	-17.3	-17.6	-17.9	-17.3 (0.48)

ORM (Observed ratio of means)=Mean body weight in SS/Mean body weight in LL, OR (Observed range)=(Mean body weight in SS-Mean body weight in LL)/Standard deviation of body weight in RR, SD : Standard deviation.

Discussion

It may be difficult to achieve a selection limit without deterioration of growth and reproductive ability, because gene diversity decreases with repeated selection, and resulting decline in biological functions may make it difficult to maintain a population. SS line might be sensitive to environmental factors as compared to RR line. Moreover, the selection for small body weight seems to take a long period of time, so selection limit may not be reached in a short term selection. In this research, it was intended to select the genes for small body weight and make them homozygous, but maintain other genes as diverse as possible during long term of 65 generations. As the results, the distinct response was steadily realized, and the decrease in body weight was recognized as a linear type with a gentle slope. Such stable and clear responses have accumulated as a significant difference between SS and RR lines ($P < 0.01$), and a genetically fixed line with small body size was established although its reproductive ability is slightly declined.

Mean standardized selection differential, SI, was -0.33 in SS line and 0.04 in RR line over 6 generations investigated. These values indicated that the aimed selection in the direction for small body weight was effectively carried out in SS line, whereas a random mating was performed in RR line. Body weight at 6 weeks of age showed normal distribution in both SS and RR lines. Especially, kurtosis was high in males of SS line, and both skewness and coefficient of variance were very small. In addition, kurtosis and skewness in females of SS line were comparable to those in RR line. The normal distribution and maintenance of normal fertility indicate that the selection experiment was successfully carried out as originally planned. The newly established SS line would be useful for studying the evolutionary mechanisms leading to miniaturization.

Realized heritability calculated with the data for body weight at 6 weeks of age increased in SS line from 54-59 to 60-65 generations in both males and females (Table 4). Mean selection response was positive during 61-62 generations, but turned to negative during 63-65 generations (Fig. 3). Estimated heritability was generally high and its variation was large in both lines. These values indicated that genetic variation

was not constant through generations, and selection response varied widely. Especially, the variation in SS line was large. These findings suggested that the sensitivity to environmental factors should be taken into consideration and attention must be paid to the management of animals to carry out long term selection for small body weight. More improvement might still be expected because the response in the direction for small body weight was recognized during last few generations as noted above.

Falconer and Mackey (1996) have hypothesized that the limit in a long term selection is caused by disappearance of additive genetic variance, balance between artificial and natural selection and decrease in fitness, and proposed the method to estimate a selection limit. The data in the present investigation were analyzed using their method, and it was evaluated whether phenotypic response to the selection for small body weight in SS line has reached to the limit. Indices on selection limit were calculated including the data of LL line selected for large body size by the same breeding method as SS line. Okamoto *et al.* (1989 a, b) concluded that the LL line reached to the selection limit at about 50th generation. This finding and the result in the present study that ORM value decreased in both males and females from 60 to 65 generations indicate that SS line may not have reached to the selection limit. Moreover, increase in absolute OR value during 60–65 generations may be due to the small but significant selection response in SS line. Therefore, SS line may not have reached to the selection limit, and more genetic gain for small size may be expected. Generally, artificial selection during very long term such as 65 generations would get into an ineffective state with no further improvement on account of limited pool for genetic diversity. It is, therefore, inferred that the selection for small body size may be achieved by small and cumulative effects of a gentle linear type differing from the selection for large body size. Miniaturization of body size is a remarkable biological process as an aspect of evolution. It is interesting to find out whether any specific changes would happen in molecular biologic and metabolic aspects accompanied with miniaturization of body size. The SS line established in the present study will contribute to the investigation in this direction.

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