Theor Appl Genet (1988) 76:775–780

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Juvenile body weight and gonad development in a diallel cross among lines of Japanese quail (*Coturnix coturnix japonica*)

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Received April 5, 1988; Accepted July 11, 1988
Communicated by K. Sittmann

Summary. The influence of growth on the extent of heterosis for juvenile body weight and gonad development was studied in a diallel cross among two lines of Japanese quail differing in adult body size. A total of 1,096 birds (563 males and 533 females) was slaughtered between 25 and 49 days of age. Reciprocal cross differences were non-significant. Heterosis showed a curvilinear course with age peaking during early growth (body weight) and during sexual maturity (gonad percentage). Overall advanced physiological development of the crossbreds probably begins as early as during the embryonic stages and results in earlier sexual maturity. In females, heterosis for percentage gonads was biased strongly by the presence of a hard-shelled egg in the uterus.

Key words: Japanese quail – Diallel cross – Heterosis – Gonad development – Sexual dimorphism

Introduction

The term heterosis is used to describe the superiority of crossbreds over the average performance of the parental lines. The forms of expression and the theoretical models for the genetical basis underlying heterosis have been discussed by Dickerson (1973), Sheridan (1981), Hill (1982), Eisen et al. (1983), and others.

The extent of heterosis might vary because of growth phase-related changes in juvenile animals; this has been seen in chickens (Smith and Jaap 1957; Zelenka et al. 1986a) and mice (Kidwell and Howard 1969; Aumann 1986). Sefton and Siegel (1974) estimated genetic parameters of body weight throughout the growth phase in Japanese quail and suggested that the importance of genes controlling body weight may vary with age.

The present study was designed to investigate age-related differences in the expression of heterosis in a diallel cross of two unrelated lines of Japanese quail (*Coturnix coturnix japonica*). Traits closely related to reproductive fitness (e.g., egg production) have shown the greatest heterosis in crosses, whereas traits less subject to natural selection (e.g., growth) were moderate in heterosis (Dickerson 1973). Accordingly, our study focused on juvenile development of gonads and body weight.

Materials and methods

Two randombred lines L and S were used (Gerken et al. 1986). Line L was a laboratory quail line of small body size that had been imported from Ohio State University, USA, in 1966. Line S had been developed by a French breeder for commercial purposes and had undergone an unknown mode of selection for large body size. This line was first imported from France to the Experiment Station Großhüttenhof, Krefeld. In 1978, a sample of 20 males and 39 females was transferred to Bonn University. Both lines have been kept as closed populations on the same management program since their introduction to Bonn University with an average generation interval of 10 months. In the parental generation, 16-week body weight for males and females averaged 113.5 and 137.1 g respectively in line L versus 171.7 and 204.3 g in line S. Ages at 50% lay were 53 (line L) and 46 (line S) days.

For the diallel cross, 80 males and 120 females from each line were randomly assigned to group matings; sib-matings within parental lines were avoided. The mating set yielded four groups of progeny (the first letter denoting the sire line and the second, the dam line): SS, LL, SL and LS.

Chicks were raised in electrically heated brooders ($73 \times 23 \times 91$ cm^3), each brooder for one mating type. At 21 days of age, birds were separated by sex; surplus birds were culled to attain an average group size of 55 birds per cage. The birds were fed ad libitum a commercial turkey starter containing 29%

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crude protein and 11.7 MJ ME per kg until 4 weeks of age, after which the diet consisted of 18% crude protein. The lighting regimen was 16 h light and 8 h darkness throughout the study.

All birds that hatched (309, 338, 371 and 377 chicks per mating type SS, SL, LS and LL respectively) were weighed at 1, 7, 14, and 21 days of age in groups of 10 (21 days), 20 (7 and 14 days) or 40 (1 day) birds. At 25, 28, 32, 35, 40, 42, 46 and 49 days of age, about 17 males and 17 females were sacrificed at random from each mating type, resulting in a total of 1,096 birds (563 males and 533 females) examined. Birds were individually weighed before being sacrificed by cervical dislocation. The gonads were removed and weighed to the nearest 0.1 g. In females, the developmental stages of the ovarian follicles and the oviduct were examined macroscopically and scored from 1 to 6 (Table 1). Hard-shelled eggs were excised from the uterus and weighed. Gonad weight (in females both before and after egg removal) was expressed as a percentage of live body weight.

Data were analyzed by ages and across all ages by least squares procedures (Harvey 1977). The statistical model across all ages was:

$$Y_{ijkl}=\mu+M_i+S_j+A_k+(MS)_{ij}+(MA)_{ik}+(SA)_{jk}+e_{ijkl}$$

where Y_{ijkl} was the performance of the lth bird of the ith mating type and the jth sex slaughtered at the kth age. Live weights recorded as group means were analyzed by weighted least squares procedures. Comparisons among mating types were made using non-orthogonal linear contrasts (Scheffé 1970). The contrasts and estimated genetic effects are outlined in Table 2. Percentage heterosis (H%) was calculated as the percentage deviation of the mean of the reciprocal crosses from the mean of the parental lines.

Results and Discussion

Live weight

The increase in live weight across both sexes is depicted for each mating type in Fig. 1. Sexual dimorphism with females outweighing males was significant when birds were sexed at 21 days, and remained significant at all subsequent ages. This agrees with reports which describe sex differences in Japanese quail to arise between 3 and 6 weeks of age (Amano and Watanabe 1966; Collins and Abplanalp 1968; Sefton and Siegel 1974; Torges and Wegner 1984).

Reciprocal cross (contrast 2) differences were not significant, whereas the differences (contrast 1) between SS and LL were significant at all ages but hatch weight. These findings are in agreement with results from Japanese quail (Chahil et al. 1975) and chickens (Bernon and Chambers 1985), which indicate that variation in body weight is primarily due to additive genetic factors.

Across all ages percentage heterosis was low and insignificant. Percentage heterosis across both sexes by age, however, increased quickly to 8.4% at 7 days, and then steadily decreased thereafter to insignificant levels, suggesting an age-dependent trend in heterosis. Thus, during the early growth phase, physiological development was accelerated in crosses compared to pure lines. This superiority seems to begin as early as during embryonic development. Hatch weights averaged 8.3, 7.1, 8.2 and 6.8 g for mating types SS, SL, LS and LL respectively, equivalent to percent hatch weights (average hatch weight/average egg weight) of 70.4%, 69.0%, 69.8% and 66.0%. These values agree with results reported by Marks (1975) that quail from lines selected for rapid growth to 4 weeks had higher percent hatch weights than non-selected quail chicks, an indication of faster embryonic development. Comparable developmental advances occurred in our crossbreds having a similar percent hatch weight.

Table 1. Classification of gonad development in females

Stage	Description
Stages of ovarian follicular development	
1	Pinkish-grey, macroscopically unstructured, smooth surface
2	White, granulated, granula < 1 mm diameter
3	White, differentiation of follicles < 2 mm diameter
4	Follicles > 2 mm diameter (begin of rapid development), at least one yellowish follicle
5	Several yellow follicles of different sizes, all < 12 mm diameter
6	Several yellow follicles, at least one > 12 mm diameter
Stages of oviduct development	
1	Not detectable with the naked eye
2	Oviduct a fine tube, < 2 mm diameter
3	Oviduct a thin tube, < 5 mm diameter, uterus muscles not developed
4	Differentiation into magnum and uterus (begin of muscle development), uterus not pigmented
5	As 4, but uterus pigmented, no follicle in oviduct
6	As 5, but soft or hard-shelled egg in uterus

Table 2. Non-orthogonal linear contrasts used in analyzing data

Contrast code	Contrast	Measures
1	SS − LL	Additive genetic effects
2	(SL♂ + SL♀) − (LS♂ + LS♀)	Reciprocal effects
3	SL♂ − LS♂	Maternal effects
4	SL♀ − LS♀	Maternal and sex-linked effects
5	SL♂ − SL♀	Sex-influenced and
6	LS♂ − LS♀	sex-linked effects
7	(SL♂ + LS♀) − (SL♀ + LS♂)	Sex-linked effects
8	(SL + LS) − (SS + LL)	Non-additive genetic effects

Similar accelerated developmental rates have been reported for crosses of chickens (Smith and Jaap 1957; Zelenka et al. 1986a) and mice (Kidwell and Howard 1969; Aumann 1986). In immature 2- and 4-week-old

Table 3. Age-related development of percentage gonads (G%, in italics after removal of egg) and heterosis (H%) by sex (least square means)

Age (days)	Males					Females				
	G% Mating type				H%	G% Mating type				H%
	SS	SL	LS	LL		SS	SL	LS	LL	
25	0.3	0.3	0.3	0.3	19.4	0.1	0.1	0.1	0.1	−4.6
28	0.4	0.5	0.6	0.4	37.4**	0.2	0.1	0.2	0.2	−6.8
32	0.8	1.0	0.9	0.7	27.7*	0.3	0.8	0.4	0.1	148.6
35	1.1	1.5	1.3	1.3	21.7	$1.5^{a,b}$	2.7^{b}	$1.6^{a,b}$	0.5^{a}	109.9*
						1.6^{a,b}	*2.5*^{b}	*1.6*^{a,b}	*0.5*^{a}	*93.4**
40	1.8	1.9	2.1	1.7	14.4	6.8	8.2	5.5	6.2	5.5
						5.3	*5.7*	*4.9*	*5.1*	*1.7*
42	1.8^{a}	$2.0^{a,b}$	2.3^{b}	1.6^{a}	30.4***	7.4	8.6	8.9	3.6	58.0**
						5.5	*5.7*	*5.9*	*3.1*	*35.0***
46	2.4	2.5	2.4	2.4	4.3	10.1	11.3	11.5	9.4	17.4
						6.2	*7.1*	*6.8*	*6.6*	*8.6*
49	2.6	2.5	2.8	2.6	3.2	11.7	10.9	11.6	10.8	0.1
						7.6	*7.0*	*7.0*	*6.7*	*−2.6*

LSQ means in the same row followed by different letters are significantly different (by sex, $P<0.05$)
* $P<0.05$; ** $P<0.01$; *** $P<0.001$

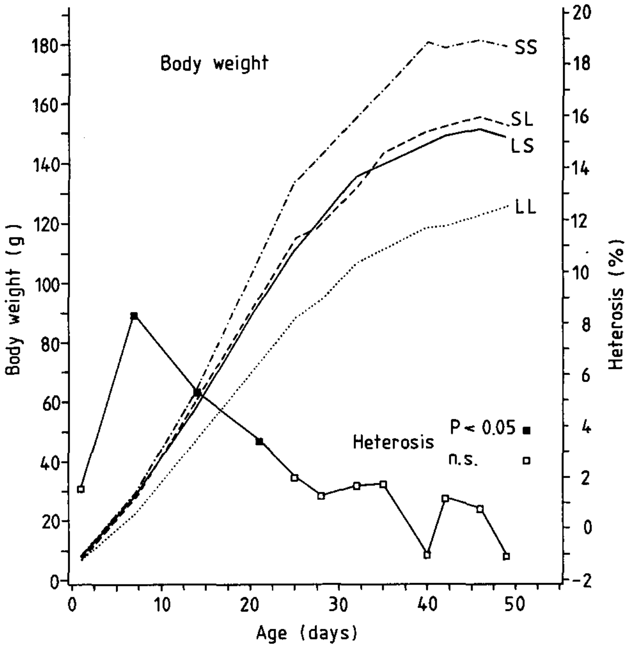

Fig. 1. Development of body weight and percentage heterosis by mating type (sexes combined)

Japanese quail, Marks (1973) and Washburn and Stino (1973) found a higher heterosis, ranging from 4% to over 9%, than was found for adult 8-week-old quail, where it ranged from −5% to 4% (Wyatt et al. 1982). An explanation for such growth-associated time trends in heterosis is that the genes controlling growth exert their influence during different phases of growth. Changes in heritability for body weight calculated for various ages in Japanese quail (Sefton and Siegel 1974) support this suggestion. These different genes may be primarily involved in the control of age-related changes in body composition such as protein and fat deposition (Zelenka et al. 1984; Zelenka et al. 1986 b).

Gonad development

In males, gonad development started at an earlier age than in females (Table 3). At 25 days of age, males had already reached about 10% of their later gonad percentage at 49 days, whereas females had only reached about 1%. At 25, 28, and 32 days, percentages of gonads were significantly higher in males than in females, thereafter, females were always significantly superior to males. These results are in agreement with those of Mather and Wilson (1964) and Amano and Watanabe (1966) who reported that males reach maturity earlier than females.

The sudden increase that we obtained in female gonad percentage between 35 and 40 days of age supports the observations of Fitzgerald (1969) and Bacon and Koontz (1971) who noted a period of rapid follicle development of 6.1 days and a short rest period of 0.09 days.

Across all mating types, development of the oviduct was slower than that of the ovarian follicles (Fig. 2). By 35 days of age, both slaces were nearly identical. Kendall's tau-b coefficients between both scales were computed as 0.0, 0.2, 0.8, 0.9, 0.9, 0.9, 1.0, and 1.0 for the ages 25, 28, 32, 35, 40, 42, 46, and 49 days respectively. These values illustrate that oviduct development is under the control of ovarian hormones (Schummer 1973) with ovary development preceding that of the oviduct. In

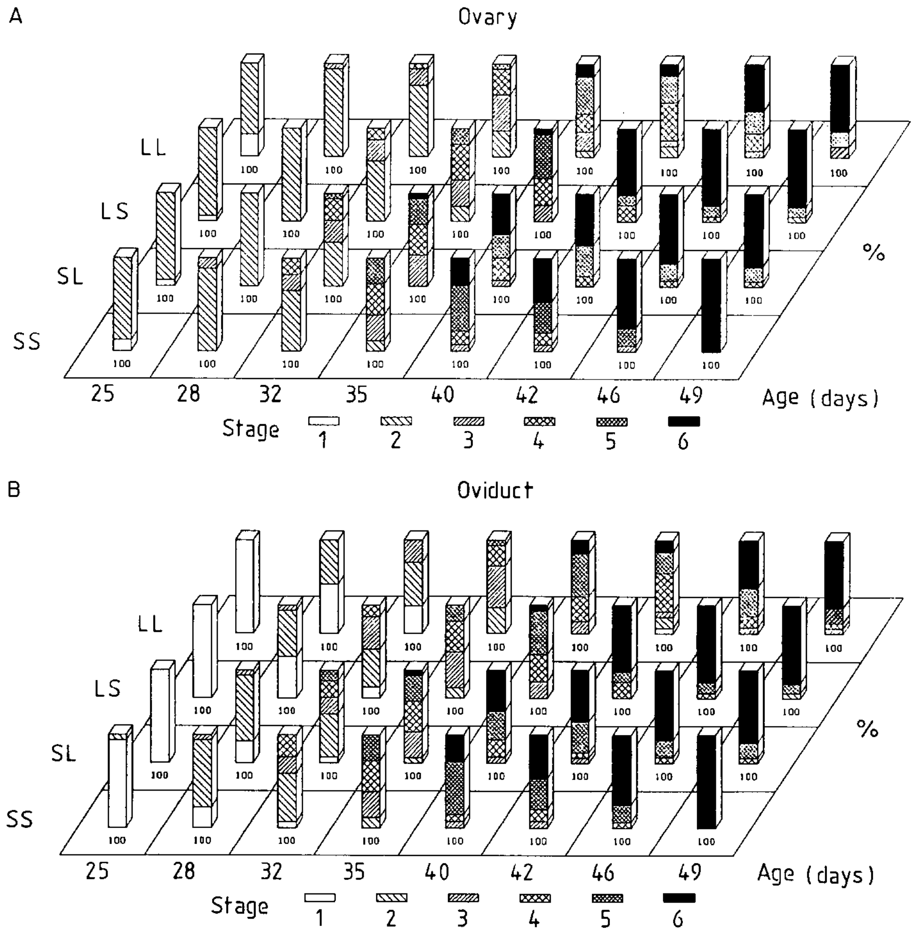

Fig. 2 A and B. Stages of ovary (**A**) and oviduct (**B**) development by mating type. Each *column* depicts the cumulative percentage of hens placed into one of the developmental classes (Table 1) for each slaughter age

Table 4. Age-associated changes in rate of hard-shelled eggs and relationship between egg, body, and gonad weights (by mating types)

Age (days)	Hens with hard-shelled eggs (%)				Egg weight as percentage of				
	SS	SL	LS	LL	Live weight				Gonads[1]
					SS	SL	LS	LL	
35	0	5.6	0	0	0	5.1	0	0	41.2
40	28.6^{a,b}	43.8^{a}	5.9^{b}	13.3^{a,b}	4.1	5.1	5.4	5.5	39.5
42	46.7^{a}	55.7^{a}	64.7^{a}	11.8^{b}	5.1	5.8	5.8	6.8	44.1
46	75.0	75.0	82.3	50.0	5.1	5.6	5.6	6.2	44.5
49	100.0	77.8	83.3	72.2	5.2^{a}	5.6^{a,b}	6.1^{b}	6.2^{b}	44.9

[1] Across all mating types

Values in the same row followed by different letters are significantly different, $P < 0.05$

crossbreds, the development of the ovarian follicles and oviduct was accelerated compared to the pure lines.

Hard-shelled eggs in the uterus occurred at an earlier age in crosses than in pure lines (Table 4). These findings agree with ages at 50% lay (across all birds, including those dissected last) which were 44, 43, 43 and 47 days for mating types SS, SL, LS and LL respectively. Since birds were housed in group cages without egg trays, it was not possible to accurately save all eggs laid, therefore, these figures are only approximate.

Egg weight, expressed as percentage of live weight, was significantly greater in the small body size L line than in the heavier S line (Table 4). Similar inter-relations between body and egg weight have been reported for growth-selected and non-selected control lines of Japanese quail (Ricklefs and Marks 1983) where selection for large body size resulted in larger eggs, but not in direct proportion to the increase in body weight.

The differences in percentage gonads (Table 3) between SS and LL were not significant for either sex (contrast 1). They were significant, however, for female gonad percentage before egg removal, underlining the influence of egg weight.

Heterosis (contrast 8) was found to be high in males by day 25, whereas in females, a sudden increase in heterosis was found at 32 days of age. In both sexes, heterosis tended to show a curvilinear course with age, an indication that crossbreds matured earlier than the parental lines. There was a strikingly sharp decrease in heterosis at 40 days of age that appeared to be compensated for by day 42. Although this decline might have been caused by chance due to the relatively small number of birds examined, we suggest that this phenomenon was due to the social interactions occurring when the birds started to develop their social hierarchy at the time of sexual maturation. Heterosis for age at 50% lay was −5.5%. Comparable negative heterosis for age at sexual maturity has also been reported for female chickens (Hagger 1985; Zelenka et al. 1986b) and Japanese quail (Wilhelmson 1980).

SL females tended to enter lay earlier than LS hens, but reciprocal effects (contrast 2) were not significant. Significant sex-influenced and sex-linked effects, however, were found (contrasts 5 and 6). Similar sex-linked effects and the influence of sire line on female gonad development have been observed in Japanese quail (Collins and Abplanalp 1968; Wilhelmson 1980). The data of Chahil et al. (1975) for age at onset of lay in Japanese quail indicate the influence of maternal effects, which in our study were not significant (contrast 4).

In females, heterosis was lower for percentage gonads after egg removal (Table 3) since egg weight accounts for about 45% (Table 4) of the gonad weight. Thus, heterosis in gonad percentage in juvenile female Japanese quail is a complex interrelationship between both sexual maturity and laying rate. Since the weight of a hard-shelled egg in the uterus can amount to more than 5% of live body weight, differences between populations in live body weight may be biased if the females were examined during the time of oviposition. According to Opel (1966), quail kept on a light schedule of 14 h light and 10 h darkness laid 80% of their eggs during the last 7 h of light. Recording body weight of females before the peak in oviposition will reduce the possible bias caused by differences in oviposition time.

In our study, the crossbreds had accelerated developmental rates which were evident in both juvenile body weight and gonad development. Since data for body weight to 3 weeks were based on a group weighing basis, the following conclusions will need further support by experimental data. We suppose that the superiority of the crossbreds is the expression of an overall advanced physiological development which presumably starts in the embryonic stages. The curvilinear course of heterosis indicated that this advancement may be mainly restricted to phases of intense growth; this is illustrated by the peaks in heterosis during the phase of most intensive growth (El-Ibiary et al. 1966; Torges and Wegner 1984) and onset of gonad development. The time-shift in heterosis for body weight and for sexual maturity illustrates that the extent of heterosis may depend on the physiological state of the birds examined. During the onset of sexual development, complex interactions between the differential genes controlling body weight and gonads may occur which should be taken into consideration, particularly in females (Sefton and Siegel 1974).

Acknowledgements. The authors wish to thank Mr. K. Sehlbach for technical assistance.

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