

A Growth Performance and Nonlinear Growth Curve Functions of Large- and Normal-Sized Japanese Quail (*Coturnix japonica*)

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This study aimed to evaluate the differences between the growth patterns of large- and normal-sized Japanese quail strains and their F_1 progeny, by fitting their growth parameter values to five nonlinear regression growth models (Weibull, Logistic, Gompertz, Richards, and Brody). The Richards model presented the best fit for both sexes of the large-sized quail strain, whereas the Gompertz model presented the best fit for both sexes of the normal-sized quail strain, based on goodness-of-fit criteria (higher adjusted R^2 and lower Akaike and Bayesian information criteria). Both sexes of F_1 birds derived from the cross between normal-sized females and large-sized males were best fitted by the Richards model. In contrast, growth parameters of the F_1 birds derived from the cross between large-sized females and normal-sized males were best fitted to the Gompertz model. The data could be fitted nearly as well to the Weibull and Logistic models as to the Richards and Gompertz models. The Brody model presented the poorest fit for the growth parameter values. The results indicated that the Richards and Gompertz models could best describe the growth characteristics of both large- and normal-sized quails. Moreover, the observed growth pattern of the F_1 birds was likely inherited from the male parental strain. To the best of our knowledge, this is the first study comparing the growth curves of the reciprocal F_1 generations with their parental strains in quails.

Key words: body weight, growth curve, Japanese quail, large-sized quail strain, normal-sized quail strain

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Introduction

Bird growth is a vital quality criterion for industrial poultry producers. It involves changes in the size, shape, weight, and volume of the animals, and is influenced by genetic and environmental factors (Sezer and Tarhan, 2005a). Growth variation is evaluated by fitting growth curve models to the body weight measurements. In poultry science, growth curve models provide useful information on animal management and health, age at sexual maturity, appropriate slaughter age, and effects of genetic improvements (Kaplan and Gürcan, 2018).

The Japanese quail (Coturnix japonica) is a model bird species for biological research (Minvielle, 2004; Jeke et al., 2018) and meat/egg production studies (Tsudzuki, 2008), due to its small size, high production efficiency, rapid generational turnover, and sexual maturity at an early age of ~6 wk (Padgett and Ivey, 1959; Woodard et al., 1973; Cain and Cawley, 1974; Ernst, 1978). Several nonlinear growth models, such as Gompertz (Gompertz, 1825), Logistic (Blumberg, 1968), Richards (Richards, 1959), Weibull (Weibull, 1951), Brody (Saeid Bathaei and Leroy, 1998), von Bertalanffy (von Bertalanffy, 1957), and Hyperbolastic (Tabatabai et al., 2005), have been developed to describe Japanese quail growth patterns. The Gompertz, Logistic, and von Bertalanffy models have fixed inflection points and present sigmoidal curves. The Brody model has a diminishing return behavior. The Richards model has a flexible

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inflection point and four parameters. There are conflicting results regarding the most suitable model for describing Japanese quail growth, in terms of the strain, line, and sex (Akbaş and Yaylak, 2000). Several studies have reported that the Gompertz model is the best suited, based on its goodness-of-fit criteria (Narinc *et al.*, 2010; Santos *et al.*, 2018). However, the Richards, Logistic, Weibull, and Brody models have also been successfully fitted to Japanese quail growth data (Karaman *et al.*, 2013; Raji *et al.*, 2014a; Abdallah, 2017).

Large-sized (LS) Japanese quail are characterized by their relatively high body weight (~200 g for females and ~170 g for males at maturity) and are used primarily for meat production. Normal-sized (NS) Japanese quail are distinguished by their normal body weight range (~130 g for females and ~100 g for males at maturity) and are used mainly for egg production (Kirkwood and Hubrecht, 2010). Reciprocal matings between these two strains yield quails with heterozygous characteristics and good growth rates. Several previous studies have focused on the growth rate of Japanese quail (Telekan et al., 2017; Faraji-Arough et al., 2018); however, to the best of our knowledge, no studies have compared the growth curves of the reciprocal F_1 generation with those of their parents, which differ genetically in terms of the trait of interest. The aim of the present study was to evaluate the differences between the growth patterns of LS and NS quails, by fitting the growth metrics of these two quail strains and their reciprocal F₁ progeny to five different nonlinear regression growth models (Weibull, Logistic, Gompertz, Richards, and Brody).

Materials and Methods

Experimental Birds

LS and NS quails were reared at the research farm of Hiroshima University, Higashi-Hiroshima, Japan. One hundred quails from each of the two strains and 50 birds from each of their reciprocal F_1 generations were used in this study. The F_1 birds were obtained by reciprocal matings between one male and three females. The body weights of all birds were measured weekly, from hatching up to the age of 16 wk. Newly hatched chicks were leg-banded and weighed before being transferred to heated brooders, where they were reared until the age of 4 wk. Thereafter, they were housed in individual cages (depth 15 cm, width 18 cm, height 18 cm). Chicks were fed a standard chick diet (22% crude

protein (CP); 2,900 kcal metabolizable energy (ME) kg⁻¹), available *ad libitum*, from 0 to 4 wk of age, and then with a grower diet (17% CP; 2,850 kcal ME kg⁻¹) from 4 to 16 wk of age. The birds were maintained under a 24-h photoperiod for 4 wk, and then under a 14 h:10 h light:dark cycle. The birds were reared following the protocol described in the Guidelines for Proper Conduct of Animal Experiments (Science Council of Japan, 2006).

Statistical Analysis and Model Comparison

The mathematical expressions for growth rate and age and weight at inflection points of the Weibull, Logistic, Gompertz, Richards, and Brody growth models are presented in Table 1. For all equations, y is the body weight at a given age, x is the time duration, a is the asymptotic weight, b and c are constants for the initial body weight and instantaneous growth rate, respectively, and d is the shape parameter in the Weibull and Richards models.

The coefficient of determination (R^2), adjusted coefficient of determination (adj. R^2), Akaike information criterion (Akaike, 1974), Bayesian information criterion (Schwarz, 1978), and root mean square error (RMSE) were used to evaluate the accuracy of the growth curve model predictions. The comparison parameters were calculated as follows:

Coefficient of determination: $R^2=1-(SSE/SST)$ Adjusted coefficient of determination: Adj. $R^2=R^2-((p-1/n-p)(1-R^2))$

Akaike's information criterion: AIC=n.ln (SSE/n)+2pBayesian information criterion: BIC=n.ln(SSE/n)+p.ln(n)Root mean square error: $RMSE=(SSE/n)^{(1/2)}$

where SSE is the sum of square errors, SST is the total sum of squares, p is the number of parameters, and n is the number of observations.

The nonlinear regression models of the growth curves were computed using the nonlinear least squares (nls) function in R v. 3.6.1. (R Core Team, 2019). The body weights of the two sexes were compared between the parental and F_1 generations and within the Gompertz and Richards models by Tukey's HSD test, in JMP v. 11.0.2 (SAS Institute Inc., Tokyo, Japan).

Results

The body weights of the LS and NS Japanese quail strains and their F_1 progeny were measured from hatching up to 16 wk (Tables 2 and 3). The body weight of LS quails was significantly higher than that of NS quails at hatching (8.19 g

Table 1. Equations for age and weight at inflection points of the growth curve models used in the present study

Model	Equation	Age at inflection point (IP_T)	Weight at inflection point (IP_W)
Weibull	$y=a-(a-b)*exp(-(c*x)^d)$	$(1/c)^{(((d-1)/d)^{(1/d)})}$	a-(a-b)*exp(-(d-1)/d)
Logistic	y=(b*a)/(b+(a-b)*exp(-c*x))	1/c*ln((a-b)/b)	a/2
Gompertz	y=a*exp(-b*exp(-c*x))	ln(b)/c	a/e
Richards	$y=(b*a)/((b^d+(a^d-b^d)*exp(-c*x))^{(1/d)})$	$-(1/c)*\ln(d/((a^d-b^d)/b^d))$	$a/((d+1)^{(1/d)})$
Brody	$y=a^{*}(1-b^{*}exp(-c^{*}x))$	—	—

y: body weight at given age; x: time duration; a: asymptotic weight; b: constant for the initial body weight; c: constant for the instantaneous growth rate; d: shape parameter.

Age (wks)	LS $\stackrel{\circ}{=}$ (<i>n</i> =50)	NS ♀ (<i>n</i> =50)	$F_1 \stackrel{\circ}{\leftarrow} (NS \stackrel{\circ}{\leftarrow} \times LS \stackrel{\circ}{\triangleleft}) $ $(n=25)$	$F_1 \stackrel{\circ}{\leftarrow} (LS \stackrel{\circ}{\leftarrow} \times NS \stackrel{\circ}{\sim}) $ (n=25)
0	8.19 ± 0.1081^{a}	6.09±0.0701°	6.89 ± 0.1948^{b}	8.54 ± 0.1156^{a}
1	27.21 ± 0.4147^{ab}	$21.29 \pm 0.3610^{\circ}$	25.62 ± 0.4885^{b}	28.52 ± 0.4235^{a}
2	56.72 ± 0.9537^{a}	$44.02 \pm 0.5758^{\circ}$	52.27 ± 1.0695^{b}	57.66 ± 0.7144^{a}
3	95.96 ± 1.4451^{a}	$71.77 \pm 0.7218^{\circ}$	88.51 ± 1.6145^{b}	94.27 ± 0.9892^{a}
4	136.58 ± 1.6558^a	$93.41 \pm 0.9440^{\circ}$	119.44 ± 1.4137^{b}	120.94 ± 1.3883^{b}
5	156.48 ± 1.7929^{a}	$110.25 \pm 1.2636^{\circ}$	140.06 ± 1.9374^{b}	144.68 ± 1.8153^{b}
6	190.49 ± 2.1768^{a}	$127.26 \pm 1.6862^{\circ}$	160.82 ± 2.4042^{b}	161.33 ± 2.4006^{b}
7	206.44 ± 2.2449^{a}	$133.40 \pm 1.8839^{\circ}$	165.45 ± 2.3364^{b}	164.41 ± 1.5985^{b}
8	211.60 ± 2.4029^{a}	$133.69 \pm 1.9436^{\circ}$	165.55 ± 2.5531^{b}	169.41 ± 2.0241^{b}
9	214.86 ± 2.6711^{a}	$138.86 \pm 1.8348^{\circ}$	166.14 ± 2.5730^{b}	170.96 ± 1.8260^{b}
10	219.96 ± 2.4104^{a}	$141.96 \pm 1.8178^{\circ}$	173.47 ± 2.5533^{b}	175.55 ± 1.9170^{b}
11	222.21 ± 2.6928^{a}	$141.79 \pm 1.7043^{\circ}$	172.07 ± 2.4935^{b}	178.06 ± 2.1360^{b}
12	221.88 ± 2.7306^{a}	$142.78 \pm 1.9305^{\circ}$	171.43 ± 2.8522^{b}	175.87 ± 2.4514^{b}
13	222.30 ± 2.8112^{a}	$142.90 \pm 1.7938^{\circ}$	173.98 ± 2.7404^{b}	179.90 ± 2.5148^{b}
14	224.78 ± 2.8199^{a}	$145.01 \pm 1.8112^{\circ}$	173.89 ± 3.0529^{b}	179.63 ± 2.4565^{b}
15	226.11 ± 3.0813^{a}	$143.52 \pm 1.8351^{\circ}$	173.80 ± 2.7708^{b}	178.86 ± 2.3888^{b}
16	225.76 ± 3.1284^{a}	$145.02 \pm 1.8940^{\circ}$	174.82 ± 2.8449^{b}	178.51 ± 2.4085^{b}

Table 2. Body weights of female LS and NS quails and their F_1 hybrids from ages 0 to 16 wk

Values are indicated as mean \pm SE. ^{a-c} Values with different superscript letters within a row are significantly different (Tukey's HSD test, $P \leq 0.05$).

Table 3. Body weights of male LS and NS quails and their F1 hybrids from ages 0 to 16 wk

Age (wks)	LS δ^{n} (n=50)	NS ∂^{n} (n=50)	$F_1 \overset{\land}{\sigma} (NS \overset{\circ}{+} \times LS \overset{\circ}{\sigma}) $ (n=25)	$F_1 \delta^{\uparrow} (LS \stackrel{\circ}{+} \times NS \delta^{\uparrow}) $ (n=25)
0	7.94 ± 0.1085^{a}	$5.91 \pm 0.1004^{\circ}$	7.00 ± 0.2084^{b}	8.41 ± 0.1381^{a}
1	24.93 ± 0.4269^{a}	19.74 ± 0.4369^{b}	25.02 ± 0.5041^{a}	26.70 ± 0.4850^{a}
2	51.52 ± 0.8122^{a}	40.58 ± 0.8742^{b}	52.32 ± 0.6438^{a}	53.79 ± 1.1689^{a}
3	88.18 ± 1.2760^{a}	67.12 ± 1.0250^{b}	86.82 ± 1.0810^{a}	86.50 ± 1.4508^{a}
4	126.25 ± 1.5340^{a}	$86.71 \pm 1.2028^{\circ}$	112.91 ± 1.2347^{b}	111.81 ± 1.6727^{b}
5	144.04 ± 1.7180^{a}	99.12±1.1275°	127.80 ± 1.4059^{b}	126.50 ± 2.1312^{b}
6	161.08 ± 1.7221^{a}	$105.18 \pm 1.0584^{\circ}$	139.47 ± 1.6887^{b}	135.30 ± 2.3824^{b}
7	172.50 ± 1.8566^{a}	$108.53 \pm 1.1249^{\circ}$	143.10 ± 1.6768^{b}	138.07 ± 2.4159^{b}
8	175.12 ± 1.7995^{a}	$110.47 \pm 1.1934^{\circ}$	141.75 ± 1.9866^{b}	139.26 ± 2.3179^{b}
9	177.95 ± 1.8264^{a}	$112.97 \pm 1.2029^{\circ}$	143.71 ± 1.9388^{b}	141.55 ± 2.3285^{b}
10	180.54 ± 1.9801^{a}	$114.14 \pm 1.2882^{\circ}$	144.36 ± 2.0119^{b}	143.79 ± 2.4521^{b}
11	183.77 ± 1.9132^{a}	$115.66 \pm 1.3473^{\circ}$	146.21 ± 2.0676^{b}	144.66 ± 2.5081^{b}
12	182.17 ± 1.8441^{a}	$116.80 \pm 1.3508^{\circ}$	147.54 ± 2.0810^{b}	146.55 ± 2.5609^{b}
13	183.26 ± 1.8740^{a}	$117.57 \pm 1.3788^{\circ}$	148.61 ± 2.2061^{b}	146.98 ± 2.5887^{b}
14	185.29 ± 1.8339^{a}	$120.02 \pm 1.3672^{\circ}$	149.14 ± 2.0725^{b}	147.31 ± 2.7661^{b}
15	186.94 ± 1.8485^{a}	$120.38 \pm 1.4489^{\circ}$	150.30 ± 2.1422^{b}	148.31 ± 3.1589^{b}
16	$188.01\!\pm\!1.9008^a$	$121.13 \pm 1.5092^{\circ}$	150.31 ± 1.8934^{b}	146.58 ± 3.1935^{b}

Values are indicated as mean \pm SE. ^{a-c} Values with different superscript letters within a row are significantly different (Tukey's HSD test, $P \leq 0.05$).

vs. 6.09 g for females and 7.94 g vs. 5.91 g for males of LS and NS strains, respectively). No significant differences could be detected between the body weights of LS and F_1 (LS $\stackrel{\circ}{+} \times NS \stackrel{\circ}{\sim}$) females from hatching up to 3 wk. The NS females exhibited the lowest body weights from hatching up to 16 wk. No significant differences were observed in the body weights of F_1 females from 4 wk of age onwards. The NS males presented the lowest body weights among all the quail generations from 0 to 16 wk of age. No significant differences were recorded between the body weights of LS and the F_1 males from the age of 1 to 3 wk. Significant differences were observed between the body weights of parental and F_1 males from the age of 4 to 16 wk. The LS and NS males presented with the highest and lowest body weights, respectively. No significant differences were detected in the body weights of F_1 males from the age of 4 wk.

Goodness-of-fit criteria for the Weibull, Logistic, Gompertz, Richards, and Brody models are shown in Table 4. The Richards model presented the best fit for both female and male LS quails (adj. $R^2=0.999$, 0.999; AIC=92.007, 81.742;

Tabl	e 4. Goodn	ess-of-fit crit	eria for the fiv	e growth mo	lels
lel	R ²	Adj. R ²	AIC	BIC	RMSE
LS Fer	nale				
11	0.999	0.998	92.983	97.149	2.778
ic	0.997	0.997	103.852	107.184	4.056
ertz	0.998	0.998	93.538	96.871	2.995
ds	0.999	0.999	92.007	96.173	2.699
	0.975	0.973	139.634	142.967	11.619
LS Ma	ıle				
11	0.998	0.998	93.050	97.216	2.784
ic	0.997	0.997	98.180	101.513	3.433
ertz	0.999	0.999	82.108	85.441	2.140
ds	0.999	0.999	81.742	85.908	1.996
	0.976	0.974	131.710	135.043	9.203
NS Fer	male				
11	0.999	0.999	74.936	79.102	1.634
ic	0.997	0.996	90.584	93.917	2.746
ertz	0.999	0.999	67.341	70.674	1.386
ds	0.999	0.999	68.734	72.900	1.361
	0.981	0.979	118.688	122.021	6.275
NS Ma	ale				
11	0.995	0.995	90.169	94.335	2.557
ic	0.993	0.993	94.328	97.661	3.065
ertz	0.994	0.993	79.516	82.849	1.983
ds	0.997	0.997	81.215	85.381	1.965
	0.982	0.981	109.324	112.657	4.764
F ₁ Fen	nale (NS ♀×I	LS 3)			
11	0.998	0.998	85.889	90.055	2.255
ic	0.998	0.997	90.811	94.144	2.764
ertz	0.998	0.998	86.568	89.901	2.440
ds	0.999	0.999	82.531	86.697	2.043
	0.973	0.971	131.062	134.395	9.030
F ₁ Mal	le (NS ♀×LS	♂)			
11	0.000	0.998	84.290	88.456	2.151
ic	0.997	0.997	87.197	90.530	2.485
ertz	0.998	0.998	78.948	82.281	1.950
ds	0 999	0 998	77 291	81 457	1 751

Table 4.

R²: coefficient of determination; Adj. R²: adjusted coefficient of determination; AIC: Akaike information criterion; BIC: Bayesian information criterion; RMSE: root mean square error.

0.974

0.998

0.997

0.999

0.999

0.979

0.997

0.997

0.998

0.999

0.978

122.884

85.731

96.221

75.623

76.338

126.051

85.215

87.965

74.466

74.397

119.025

126.217

89.897

99.553

78.956

80.504

129.383

89.381

91.298

77.799

78.563

122.357

and BIC=96.173, 85.908 for females and males, respectively). The Gompertz model exhibited the best fit for both sexes of the NS strain (adj. $R^2 = 0.999$, 0.993; AIC = 67.341, 79.516; and BIC=70.674, 82.849 for females and males, respectively). Data for the F_1 (NS $\stackrel{\circ}{\to} \times LS \stackrel{\circ}{\to}$) birds was the best fitted with the Richards model (adj. $R^2 = 0.999$, 0.998;

Model

Weibull

Logistic

Gompertz

Richards

Brody

Weibull

Logistic

Brody

Weibull

Logistic

Brody

Weibull

Logistic

Gompertz

Richards

Brody

Weibull

Logistic

Gompertz

Richards

Brody

Gompertz Richards

Gompertz Richards

0.976

 F_1 Female (LS $\stackrel{\circ}{\rightarrow} \times NS \stackrel{\circ}{\rightarrow}$)

0.998

0.997

0.999

0.999

0.980

0.997

0.997

0.999

0.999

0.979

 F_1 Male (LS $\stackrel{\circ}{\rightarrow} \times NS \stackrel{\circ}{\rightarrow}$)

AIC=82.531, 77.291; and BIC=86.697, 81.457 for females and males, respectively). In contrast, the Gompertz model presented the best fit for the F₁ (LS $\stackrel{\circ}{\rightarrow} \times NS \stackrel{\circ}{\rightarrow}$) birds (adj. $R^2 = 0.999, 0.998; AIC = 75.623, 74.466; and BIC = 78.956,$ 77.799 for females and males, respectively). All quail generations were best fitted using the Richards or Gompertz

7.099

2.244

3.241

1.768

1.703

7.792

2.211

2.542

1.709

1.608

6.338

Model	Parameter	LS $\stackrel{\circ}{=}$ (<i>n</i> =50)	NS $\stackrel{\circ}{=}$ (n=50)	$F_1 \stackrel{\circ}{\leftarrow} (NS \stackrel{\circ}{\leftarrow} \times LS \stackrel{\circ}{\triangleleft}) $ $(n=25)$	$F_1 \stackrel{\diamond}{\leftarrow} (LS \stackrel{\diamond}{\leftarrow} \times NS \stackrel{\diamond}{\triangleleft}) $ $(n=25)$
Gompertz	а	226.53 ± 2.7194^{a}	144.51±1.7641°	174.27 ± 2.5580^{b}	178.88 ± 2.0100^{b}
	b	6.0278 ± 0.1056^{ab}	5.5716 ± 0.1555^{b}	6.5714 ± 0.1860^{a}	5.5596 ± 0.1366^{b}
	с	$0.4917 \pm 0.0071^{\circ}$	0.5133 ± 0.0086^{bc}	0.5753 ± 0.0121^{a}	$0.5382 {\pm} 0.0104^{ab}$
	IP_T	3.6550 ± 0.0314^a	3.3187 ± 0.0246^{b}	3.2694 ± 0.0368^{bc}	$3.1816 \pm 0.0262^{\circ}$
	IP_W	83.337 ± 1.0004^{a}	$53.164 \pm 0.6490^{\circ}$	64.110 ± 0.9410^{b}	65.807 ± 0.7394^{b}
Richards	а	221.20 ± 2.7369^{a}	$143.73 \pm 2.0426^{\circ}$	172.37 ± 2.9994^{b}	175.46 ± 2.5181^{b}
	b	3.3941 ± 0.2910^{a}	2.0483 ± 0.2041^{b}	2.7962 ± 0.2680^{ab}	2.7560 ± 0.3090^{ab}
	с	0.6037 ± 0.0170^{b}	0.6184 ± 0.0252^{b}	0.7298 ± 0.0340^{a}	0.6427 ± 0.0240^{ab}
	d	0.4327 ± 0.0519^a	0.3301 ± 0.0664^{a}	0.5393 ± 0.0743^{a}	$0.3525 {\pm} 0.0572^a$
	IP_T	$4.0563 \!\pm\! 0.0585^a$	3.5654 ± 0.0792^{b}	3.7126 ± 0.0605^{b}	3.4893 ± 0.0613^{b}
	IP_W	95.134 ± 1.6155^a	$59.448 \pm 1.4616^{\circ}$	76.589 ± 1.8191^{b}	73.942 ± 1.6121^{b}

 Table 5.
 Values of the equation parameters and age and weight at inflection points for female quails estimated by the Gompertz and Richards models

Values are indicated as mean \pm SE. ^{a-c} Values with different superscript letters within a row are significantly different (Tukey's HSD test; P < 0.05).

a: asymptotic weight; *b*: constant for the initial body weight; *c*: constant for the instantaneous growth rate; *d*: shape parameter; IP_T : age at inflection point (wk); IP_W : weight at inflection point (g).

Table 6.	Values of the equation parameters and age and weight at inflection points for male quails estimated h	Эy
the Gom	ertz and Richards models	

Model	Parameter	LS \mathcal{J} (n=50)	NS \mathcal{J} (n=50)	$F_1 \mathcal{J} (NS \stackrel{\text{\tiny{\square}}}{\to} LS \mathcal{J})$ $(n=25)$	$F_1 \mathcal{F} (LS \stackrel{\text{$\stackrel{\circ}{\to}$}}{\times} NS \stackrel{\text{$\stackrel{\circ}{\to}$}}{\times}) $ $(n=25)$
Gompertz	а	185.46 ± 1.8273^{a}	$117.85 \pm 1.3514^{\circ}$	148.32 ± 1.9648^{b}	146.46 ± 2.6416^{b}
	b	6.3288 ± 0.1296^{a}	5.7744 ± 0.1606^{b}	6.5512 ± 0.1765^{a}	5.9672 ± 0.2398^{ab}
	с	$0.5434 \pm 0.0073^{\circ}$	0.5723 ± 0.0104^{bc}	$0.6288 {\pm} 0.0116^a$	0.6075 ± 0.0172^{ab}
	IP_{T}	3.3896 ± 0.0302^{a}	3.0418 ± 0.0288^{b}	2.9843 ± 0.0265^{b}	2.9249 ± 0.0331^{b}
	IP_W	68.227 ± 0.6722^{a}	$43.355 \pm 0.4972^{\circ}$	54.565 ± 0.7228^{b}	53.880 ± 0.9718^{b}
Richards	а	183.98 ± 2.0043^{a}	$112.02 \pm 1.9159^{\circ}$	147.36 ± 2.8801^{b}	145.16 ± 3.1394^{b}
	b	2.1132 ± 0.1896^{a}	1.7851 ± 0.1905^{a}	2.4984 ± 0.3666^{a}	2.1772 ± 0.2777^{a}
	с	0.6437 ± 0.0199^{b}	0.7633 ± 0.0232^{a}	0.8103 ± 0.043^{a}	0.7783 ± 0.0495^{a}
	d	$0.3592 {\pm} 0.0501^a$	0.4570 ± 0.0548^{a}	0.5621 ± 0.0956^a	0.4635 ± 0.102^{a}
	IP_{T}	3.7204 ± 0.0564^{a}	3.3767 ± 0.1553^{b}	3.3846 ± 0.0518^{b}	3.2205 ± 0.0602^{b}
	IP_{W}	77.522 ± 1.4486^{a}	$49.007 \pm 1.3727^{\circ}$	65.654 ± 1.5298^{b}	62.188 ± 1.4512^{b}

Values are indicated as mean \pm SE. ^{a-c} Values with different superscript letters within a row are significantly different (Tukey's HSD test; $P \le 0.05$).

a: asymptotic weight; *b*: constant for the initial body weight; *c*: constant for the instantaneous growth rate; *d*: shape parameter; IP_T : age at inflection point (wk); IP_W : weight at inflection point (g).

models, with the Weibull and Logistic models presenting a comparable fit to these models.

The estimated equation parameters and age and weight at inflection points of the Gompertz and Richards models for female and male quails are shown in Tables 5 and 6. In case of female quails, significant differences were observed in the asymptotic weights (*a*) and age (IP_T) and weight (IP_W) at inflection points of the parental generations in the Gompertz model. The LS and NS females presented the highest and lowest *a*, respectively. No significant differences were observed between the reciprocal F_1 generations for any of the parameters estimated by both models, except the initial body weight (*b*) in the Gompertz model. No significant differences were observed between the instantaneous growth rates (*c*) of the parental generations in the Gompertz and Richards models. The shape parameter (*d*) did not differ between generations. In case of males, no significant differences could be detected between the parameter values of the reciprocal F_1 generations in the Gompertz and Richards models (Table 6). The *c* value was the lowest for LS males in the Richards model. The estimated values for *a*, IP_T, and IP_W in both models were the highest for LS males. The *b* and *d* values in the Richards model did not differ between generations.

The Gompertz and Richards models for the LS, NS, and reciprocal F_1 generations are shown in Fig. 1. The Gompertz and Richards IP_T for both LS sexes was observed to be higher than that for the NS and F_1 quails (3.6550 wk vs. 4.0563 wk for the Gompertz and Richards models, respectively, in females, and 3.3896 wk vs. 3.7204 wk for the Gompertz and Richards models, respectively, in males). No significant differences were observed between the Gompertz and Richards IP_T values of both NS and F_1 quail sexes,



Fig. 1. Gompertz and Richards models for the two sexes of the LS and NS quails and their reciprocal F_1 progeny. LS and NS indicate large- and normal-sized quail strains, respectively.

except for the NS and F_1 (LS $\stackrel{\circ}{\to} \times NS \stackrel{\circ}{\to}$) females in the Gompertz model. Both sexes of the LS and NS quails exhibited the highest and lowest IP_W values, respectively, in the Gompertz and Richards models. The F_1 birds presented intermediate body weights when compared with those of their LS and NS parents from ages 4 to 16 wk.

Discussion

Our results demonstrated that the Gompertz model presented the best fit for NS and F_1 (LS $\stackrel{\circ}{\rightarrow} \times NS \stackrel{\circ}{\rightarrow}$) birds among all the five models examined. Faraji-Arough *et al.* (2018) and Santos *et al.* (2018) have previously reported that the Gompertz model is the most suited for plotting Japanese quail growth curves. However, the Richards model includes more parameters and possesses greater flexibility than the other growth models (Yin *et al.*, 2003), and presented the best fit for LS and F_1 (NS $\stackrel{\circ}{\rightarrow} \times LS \stackrel{\circ}{\rightarrow}$) quails in the present study. These results were consistent with those of previous studies evaluating Japanese quail growth (Sezer and Tarhan, 2005b; Beiki *et al.*, 2013; Teleken *et al.*, 2017; Kaplan and Gürcan, 2018). Goto et al. (2011), Norris et al. (2007), and Raji et al. (2014b) further reported that the Gompertz model is the best for describing Galliformes and Japanese quail growth. However, some studies support that both the Gompertz and Richards models can effectively illustrate Japanese quail growth patterns (Akbaş and Oğuz, 1998; Sezer and Tarhan, 2005a; Alkan et al., 2009; Narinc et al., 2010; Firat et al., 2016). In the present study, the Weibull and Logistic growth models fit nearly as well as the Gompertz and Richards models. Abdallah (2017) reported that the Logistic model best described the growth in LS and control Japanese quail lines. The Brody model yielded the poorest results in the present study. It has previously been reported that the Brody model is the most suited for ruminants (Marinho et al., 2013; Simanca et al., 2017; Kheirabadi and Rashidi, 2019), which require a longer time period to reach their mature body weight, when compared with Galliformes. These observations corroborate the results of studies on mathematical models used to describe Japanese quail growth (Teleken et al., 2017). Data for the F₁ (LS $\stackrel{\circ}{\rightarrow} \times$ NS $\stackrel{\circ}{\rightarrow}$ and NS $\stackrel{\circ}{\rightarrow} \times$ LS \mathcal{J}) birds could be best fitted by the Gompertz and Richards models, respectively, in the present study. Our results suggest that male birds may be primarily responsible for inheritance of traits from parental lines.

The Gompertz and Richards models include three and four parameters, respectively, and were employed to describe the differences between the growth patterns of the NS and LS birds and their F_1 hybrids. The *a* values were higher for females than for males for both parental strains and their F₁ progeny. Unlike other Galliformes, this finding was expected for quails, and was consistent with a previous report modeling Japanese quail growth (Karaman et al., 2013). The *a* values in the Richards and Gompertz models for the Japanese quails under study were lower than those previously reported (Kaplan and Gürcan, 2018). Several studies have reported a values between 174.0 g and 244.7 g obtained using nonlinear growth models for Japanese quail (Kizilkaya et al., 2006; Alkan et al., 2012; Gürcan et al., 2017), which are consistent with those obtained in the present investigation. The *a* value is contingent upon genetic and environmental factors (Raji et al., 2014b), and thus, it is expected to vary for quails with distinct genotypes and those reared under diverse environmental conditions. The estimated values of b in the Gompertz and Richards models were higher than those previously reported (Narinc et al., 2010; Kaplan and Gürcan, 2018), and those in the Gompertz model were not consistent with the values reported for quail lines selected for high and low body weight at 6 wk of age (Abdallah, 2017). It is evident from Fig. 1 that the c curve was S-shaped, as the parameter value changed as the quails approached their mature weight. This parameter value was higher for males than for females across all generations. Males attained their mature weight at inflection point and asymptotic weight earlier than females. These findings are consistent with those obtained by a growth curve analysis of divergently selected Japanese quail (Kizilkaya et al., 2006). Aggrey (2003) studied the effect of sex on growth rate parameters. The estimated values for parameter c in the present study were not consistent with those obtained in a previous study on nonlinear growth models for Japanese quails (Sezer and Tarhan, 2005a). In quail, the growth period and a value increase as the c value decreases. Similar results for a and c have been previously reported (Karaman et al., 2013), whereas Aggrey (2009) estimated relatively higher c values for male and female quails using mixed-effects Logistic models. The d values in the Richards model were higher for males than for females across all generations, except for LS quails. Similar results were reported by Sezer and Tarhan (2005a) in their study on meat-producing quail growth curves.

The age and weight at inflection points of LS quails in the Gompertz and Richards models were 3.6550 vs. 4.0563 wk and 83.337 vs. 95.134 g, respectively, for females, and 3.3896 vs. 3.7204 wk and 68.227 vs. 77.522 g for males, respectively. Kaplan and Gürcan (2018) reported comparatively higher weight at inflection points of Gompertz and Richards models (105.84 vs. 107.44 g, respectively, for females, and 81.96 vs. 82.88 g, respectively, for males). They

also reported similar or relatively lower values for age at inflection points of the Gompertz and Richards models (25.05 vs. 25.29 d, respectively, for females, and 21.20 vs. 21.30 d, respectively, for males). The age and body weight at inflection points of the Gompertz model for a control Japanese quail line have previously been reported as 2.8193 wk and 72.51 g (Abdallah, 2017). These findings are inconsistent with those of the present study. The age at inflection point estimated for Japanese quail using the Gompertz model by Gürcan *et al.* (2017) was higher than that determined in the present study. These discrepancies may be attributed to the differences in the growth period included in the previous studies; in the present study, quails were reared until 16 wk of age.

The two sexes exhibit different growth characteristics across generations, which is known as sexual dimorphism. Hyánková et al. (2001), Aggrey (2003), and Kizilkaya et al. (2006) have previously reported sexual dimorphism in Japanese quail. The present study did not indicate any influence of sex on hatching weight across all generations. Sex differences were observed at 1 wk of age in all generations, except for the F₁ (NS $\stackrel{\circ}{\rightarrow} \times$ LS $\stackrel{\circ}{\rightarrow}$) generation. The distinct sexual phenotype of this generation had manifested by the age of 4 wk. These observations were different from those reported by Ashok and Prabakaran (2012). They observed a significant effect of sex on body weight between ages 1 and 6 wk. In contrast, Sezer and Tarhan (2005a) did not report any sex differences in quails raised for meat; however, they observed sex differences at 15 d of age in the wild type quails.

Our findings provide a holistic idea of age at sexual maturity and appropriate slaughter age for Japanese quail. The results indicated that the male parental strain played a key role in the inheritance of characteristics in the F_1 offspring. This is the first report on the effect of male parents on the mode of inheritance of growth traits. Further studies on growth performance traits are required prior to their application in developing poultry breeding strategies. The quantitative trait loci (QTL) for growth curve parameters of Japanese quail have not yet been studied. Hence, our results provide the basis for future QTL analyses to understand the genetic basis of variation in growth curve parameters.

Here, we demonstrated that the Richards model is the most suitable for describing growth patterns of the LS and F_1 (NS $\stackrel{\circ}{+} \times LS \stackrel{\circ}{\wedge}$) quails, whereas the growth measurements of the NS and F_1 (LS $\stackrel{\circ}{+} \times NS \stackrel{\circ}{\wedge}$) quails can be best fitted with the Gompertz model. The growth patterns observed in the F_1 birds were likely inherited from the male parental strain.

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Conflicts of Interest

The authors declare no conflict of interest.

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