

# ANATOMICAL RESPONSE TO SELECTION FOR FOUR-WEEK BODY MASS IN JAPANESE QUAIL

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**ABSTRACT.**—We analyzed changes in masses, proportions, and water contents of components of Japanese Quail (*Coturnix japonica*) following long-term selection for 4-week body mass. Chicks from selected and control lines were sacrificed at 0, 1, 2, 4, 6, and 9 weeks of age and dissected into 12 components, including plumage, major muscle masses, visceral organs, and brain. Selection for 40 generations had led to more than a doubling in mature mass and a 26–28% decrease in the time required to achieve that size. The difference in growth rates was expressed only before the age of 2 weeks post-hatching, hence before chicks had achieved 50% of mature mass. Proportions of several organs and components during the growth period were not markedly affected, but the mass of the pectoral muscles of the selected chicks increased, and the mass of the brain and the wing area decreased, relative to body size. The absolute growth of the brain did not differ between lines. There were no differences between lines in the relative water contents of tissues of chicks of similar ages. These results suggest that growth rate can be increased without decreases in the apparent levels of functional maturity of tissues or changes in body proportions that lead to a decrease in the growth increment of a constraining tissue. Received 3 April 1984, accepted 4 October 1984.

THE fitting of sigmoid equations to growth data has allowed ornithologists to make comparisons among species based on estimates of growth-rate constants ( $K$ ; Ricklefs 1968a, 1973; Dunn 1975; Case 1978). Such analyses have revealed patterns in growth-rate variation associated with adult body size, mode of development, adult anatomical proportions, and ecological circumstance (Ricklefs 1979b). There is, however, no general agreement on the selective factors and biological constraints that underlie these patterns (Ricklefs 1969, 1979b; Case 1978; O'Connor 1978; Dunn 1980). Several hypotheses that account for variation in growth-rate constants among species are plausible:

(1) Growth rate may be optimized with respect to opposing selective factors of mortality and brood size, the latter mediated by the relationship of chick energy requirement to growth rate (Lack 1968, Case 1978, Ricklefs 1984a). Factors favoring more rapid growth include predators, adverse weather, and sibling competition (Werschkul and Jackson 1979).

(2) Among species whose young are self-feeding (i.e. precocial species) or that have broods of only one chick (i.e. most pelagic species), mortality factors may select increased growth rate up to a value determined by the

availability of energy or essential nutrients in food (Ricklefs 1984a). Nutritional limits to growth rate in poultry are suggested by the effects of protein levels on growth (Marks 1978c, Clark et al. 1982) and heritabilities and selection responses of body mass (Marks and Britton 1978).

(3) An upper limit to growth rate may be set by the rate at which food can be digested and assimilated (Ricklefs 1969, O'Connor 1975). This hypothesis gains considerable support from experiments with force-feeding of domestic fowl, in which growth rate is accelerated only after hypertrophy of the visceral organs (Nir et al. 1974, 1978).

(4) An upper limit to growth rate may be set by the rate at which the cells in tissues can proliferate (Ricklefs 1969). This hypothesis is supported by a close inverse correlation between growth rate and precocity of development predicted by the hypothesis (Ricklefs 1979a).

(5) A small part of the variation in growth rate among species may represent differences in the timing of the rapid-growth phases of different tissues, especially the plumage (Ricklefs 1968b), or of the deposition and utilization of fat stores.

Part of the difficulty in distinguishing among these hypotheses has been that they are all plausible and they are not mutually exclusive. Indeed, economy of design would seem to dictate that if one factor predominated in setting a limit to growth rate, other factors would become adjusted to the same limit. For example, if tissue-level constraints set a lower limit to growth rate, the size of the food-processing organs might be reduced until they were just large enough to assimilate the nutrients required for growth. Or, if mortality factors decreased so as to reduce the optimum growth rate, precocity of development might be increased, itself setting a lower limit to growth rate, so that the chicks might be thermally less dependent and allow their parents more foraging and self-maintenance time.

Because growth rate has a large heritable component (Kinney 1969, Marks 1978b; cf. Ricklefs and Peters 1979, Ricklefs 1984b), differences among species are probably in large part genetic (cf. James 1983), and it is difficult to disentangle the effects of various factors acting to promote the observed variation. One promising approach lies in the comparison of lines of organisms selected for rapid or slow growth with unselected controls. Analysis of the response to strong selection should enable one to determine whether growth is limited by a single attribute or by several potentially limiting attributes that are mutually adjusted to the same level of growth restriction.

In this paper, we examine anatomical differences between a line of Japanese Quail (*Coturnix japonica*) selected for 4-week body mass and an unselected control line. Over 40 generations of selection have resulted in a marked increase in 4-week body mass (Marks and Lepore 1968, Marks 1978b). This increase resulted in part from an increase in the mature size of the individual (over 100%) and in part from an increase in the rate at which mature size is attained (about 40%; Marks 1978a). Because the mass of the egg of the selected strain increased by only 20% over that of the control (Marks 1979), the mass of the egg yolk by 8% (Ricklefs and Marks 1983), and the mass of the neonate by 28% (Ricklefs and Marks 1984), selection primarily affected postnatal growth.

Fowler et al. (1980) determined that pectoral (*pectoralis major* and *supracoracoideus*) muscles and the *semimembranosus* muscle of the leg did not differ markedly in composition and struc-

ture of muscle fibers in the selected and control lines of the Japanese Quail used in this study. Instead, the increase in muscle mass in response to selection for 4-week body mass (between 2- and 3-fold over controls) was due primarily to increase in mass of a basic muscle structure that is qualitatively similar in both lines. Muscles of the selected line did increase in proportion to the rest of the body over their proportions in the control line. In addition to such changes in body proportions, the relative numbers of alpha and beta fibers and the relative numbers of satellite cell nuclei in the *semimembranosus* muscle also changed as a result of selection (Fowler et al. 1980, Campion et al. 1982). In contrast, however, the brains of the selected and control lines did not differ in absolute mass, hence the relative mass of the brain decreased markedly following selection (Ricklefs and Marks 1984).

Each of the hypotheses presented above makes different predictions about anatomical changes in selected chicks. Compared to controls, the first hypothesis, based on optimization of growth rate to balance primarily ecological factors, would not predict major changes in proportions, biochemical composition, or cellular architecture of tissues. The second hypothesis, based on ecological limits imposed by food resources, probably is not applicable to strains of domesticated birds maintained for generations on *ad libitum* rations of high-quality food. The third hypothesis, based on limitations of food digestion and assimilation, would predict an increase in the relative size or mass-specific level of function of visceral organs in selected lines during the period of most rapid growth.

The fourth hypothesis, based on cellular limitations of the rate of tissue proliferation, would predict an increase in the relative size of limiting tissues prior to the period of greatest growth differences or a delay in the maturation of tissue function to increase the proportions of proliferating cells. Based on comparisons of altricial and precocial birds, Ricklefs (1979a, b) suggested that leg muscles are likely to be a limiting tissue. Following upon their analysis of the relationship between gestation period and neonatal brain mass in mammals, Sacher and Staffeldt (1974) suggested that the growth rate of the brain might set the ultimate limit to the growth rate of vertebrate individuals. The fifth hypothesis predicts differences in the pat-

TABLE 1. Lengths (mm) of certain appendages and structures and area (cm<sup>2</sup>) of the wing of C and P chicks between hatching and 9 weeks. Ratios of successive lengths and of C and P lines are also presented.

Structure	Line	Measurement $X_i$ at age $i^*$												
		$X_0$	$X_1/X_0$	$X_1$	$X_2/X_1$	$X_2$	$X_3/X_2$	$X_3$	$X_4/X_3$	$X_4$	$X_5/X_4$	$X_5$	$X_6/X_5$	$X_6$
Wing	C	<b>14.8</b>	2.82	<b>41.9</b>	1.60	<b>67.0</b>	1.45	<b>97.3</b>	1.10	<b>106.8</b>	0.96	<b>103.0</b>		
	P	<b>12.3</b>	3.62	<b>44.5</b>	1.80	<b>80.0</b>	1.32	<b>105.3</b>	1.12	<b>118.3</b>	0.90	<b>106.8</b>		
	P/C	0.83	1.28	1.06	1.13	1.19	0.91	1.08	1.02	1.11	0.94	1.04		
Fifth primary	C	—	—	<b>34.0</b>	1.30	<b>44.3</b>	1.38	<b>61.3</b>	1.11	<b>67.8</b>	0.90	<b>61.0</b>		
	P	—	—	<b>34.8</b>	1.58	<b>55.2</b>	1.31	<b>72.3</b>	1.00	<b>72.0</b>	0.86	<b>62.3</b>		
	P/C	—	—	1.02	1.22	1.25	0.95	1.18	0.90	1.06	0.96	1.02		
Outer primary	C	—	—	<b>25.9</b>	1.62	<b>42.0</b>	1.31	<b>54.9</b>	1.47	<b>80.5</b>	0.78	<b>62.5</b>		
	P	—	—	<b>25.0</b>	2.0	<b>52.5</b>	1.19	<b>62.3</b>	1.34	<b>83.3</b>	0.87	<b>72.3</b>		
	P/C	—	—	0.97	1.29	1.24	0.91	1.13	0.91	1.03	1.12	1.16		
Wing area	C	—	—	<b>16.1</b>	2.10	<b>33.8</b>	1.73	<b>58.6</b>	1.52	<b>88.5</b>	0.83	<b>73.7</b>		
	P	—	—	<b>17.8</b>	3.17	<b>56.3</b>	1.63	<b>91.6</b>	0.82	<b>75.2</b>	1.07	<b>80.1</b>		
	P/C	—	—	1.10	1.51	1.67	0.94	1.56	0.54	0.85	1.28	1.09		
Tarsometatarsus	C	<b>15.5</b>	1.23	<b>19.0</b>	1.21	<b>22.9</b>	1.32	<b>30.2</b>	1.10	<b>33.2</b>	0.84	<b>28.0</b>		
	P	<b>15.7</b>	1.43	<b>22.3</b>	1.47	<b>32.8</b>	1.17	<b>38.5</b>	0.99	<b>38.3</b>	0.91	<b>34.8</b>		
	P/C	1.01	1.16	1.18	1.21	1.43	0.89	1.28	0.90	1.15	1.08	1.24		
Tibiotarsus	C	<b>15.2</b>	1.32	<b>20.0</b>	1.41	<b>28.1</b>	1.50	<b>42.1</b>	1.03	<b>44.8</b>	1.01	<b>45.0</b>		
	P	<b>13.9</b>	1.73	<b>24.0</b>	1.51	<b>36.3</b>	1.39	<b>50.5</b>	1.15	<b>58.3</b>	0.90	<b>52.5</b>		
	P/C	0.92	1.31	1.20	1.08	1.29	0.93	1.20	1.08	1.30	0.90	1.16		
Humerus	C	<b>7.0</b>	1.90	<b>13.3</b>	1.69	<b>22.6</b>	1.36	<b>30.7</b>	1.08	<b>33.1</b>	1.00	<b>33.0</b>		
	P	<b>7.5</b>	2.16	<b>16.2</b>	1.76	<b>28.4</b>	1.30	<b>37.0</b>	1.06	<b>39.4</b>	1.04	<b>41.0</b>		
	P/C	1.07	1.13	1.21	1.04	1.26	0.96	1.21	0.99	1.19	1.04	1.24		

\* Boldface numbers represent measurements; other numbers are calculated ratios.

terns of lipid deposition or rapid-growth periods of certain organs that cause the growth rate of the individual as a whole to appear faster or slower.

Here we report the proportions and water contents of organs and components of selected and control lines of Japanese Quail in an attempt to evaluate these hypotheses. Water content is assumed to provide a general index to tissue function, generally decreasing as enzymes and structural proteins accumulate in tissues with increasing mass-specific function (e.g. Ricklefs and Webb 1985).

#### METHODS

Anatomical observations are based upon quail lines P and C (Marks 1978b). Line P had been selected for 47 generations for high 4-week body mass on an adequate (28%) protein diet. The nonselected control line (C) also was reared on an adequate (28%) protein diet and treated identically to the selected P line in other respects. We sacrificed 3–6 chicks of each line at each of 0, 1, 2, 4, 6, and 9 weeks post-hatching and froze them for subsequent analysis. Each of the thawed specimens was measured to determine the lengths of the folded wing, tarsus, fifth primary

feather, and outer primary feather and the area of the wing. The specimens were then dissected into 12 components: plumage, skin, brain, head (brain removed), leg, leg muscles, pectoral muscles (*pectoralis major* and *supracoracoideus*), wings, heart, liver, gizzard (contents removed), and remaining carcass. Each component was air-dried at 60°C and extracted for at least 24 h in each of 2 baths of a 5:1 mixture of petroleum ether and chloroform. The extracted components were combusted in a muffle furnace at 500°C. We then measured the lengths of the ashed humerus, tarsometatarsus, and tibiotarsus. In this paper, water = fresh mass – dried mass, lipid = dry mass – extracted mass, lean mass = extracted mass + water (or, alternatively, fresh mass – lipid), and percent water = (water/lean mass) × 100.

Statistical analyses follow Sokal and Rohlf (1981), employing procedures of the Statistical Analysis System (SAS, Helwig and Council 1979). Details of the analyses are presented in the Results section.

#### RESULTS

*Lengths of appendages.*—The lengths of the wing, tarsometatarsus, humerus, and tibiotarsus of neonates did not differ (*t*-test) between the P and C lines (Table 1). Over the subsequent weeks, however, these appendages in-

TABLE 2. Parameters (SE) of Gompertz equations fitted to constituents of Japanese Quail chicks selected for 4-week body mass, and controls.

	Control (C) <sup>a</sup>	Selected (P) <sup>b</sup>	Ratio (P/C)
Asymptote (g)			
Wet	127.5 (5.1)	271.7 (8.4)	2.13
Water	72.3 (3.3)	154.5 (5.9)	2.14
Lean	32.4 (1.1)	69.4 (2.4)	2.10
Lean wet	106.6 (4.3)	223.8 (8.5)	2.10
Growth rate (day <sup>-1</sup> )			
Wet	0.075 (0.007)	0.096 (0.010)	1.28
Water	0.083 (0.010)	0.120 (0.019)	1.45
Lean	0.094 (0.009)	0.090 (0.010)	0.96
Lean wet	0.086 (0.010)	0.108 (0.015)	1.26

<sup>a</sup> n = 35.

<sup>b</sup> n = 26.

creased more rapidly in the P line, so that by 4 weeks the average length of tarsometatarsus of P chicks (33.4 mm ± 0.6 SE) was 28% greater than that of C chicks (26.7 mm ± 0.6), that of the humerus was 21% greater (37.0 mm ± 0.8 vs. 30.7 mm ± 1.0), and that of the tibiotarsus was 20% greater (50.5 mm ± 1.0 vs. 42.1 mm ± 0.7). It was also evident that feathers of P chicks grew more rapidly after 1 week than those of C chicks, but extreme feather wear after 4 weeks caused feather length to decrease and made comparisons between the two lines uninterpretable. At 4 weeks, the wing area of P chicks (91.6 cm<sup>2</sup> ± 5.5 SE) was 56% greater than that of C chicks (58.6 cm<sup>2</sup> ± 3.2). But when divided by the mass of the chick, the relative wing area in the P line at 4 weeks was only 63% of that of the C line. Nine-week-old P-line chicks (288 g ± 10 SE) weighed 2.22 times as much as C-line chicks the same age (141 g ± 12). If linear dimensions were scaled according to the cube root of mass, one would expect measurements of the appendages of P-line chicks to exceed those of C-line chicks by about 30%.

*Growth-rate parameters.*—We fitted Gompertz equations (NLIN procedure of SAS) to masses of fresh, aqueous, extracted, and lean components of whole chicks. The Gompertz equation relating mass (*M*) to age (*x*) is sigmoid in form and may be written

$$M(x) = A \exp\{-\exp[-K(x - I)]\},$$

where *A* is the asymptote or mass plateau (g), *K* is the growth-rate constant (day<sup>-1</sup>), and *I* is the age (days) at the inflection point, i.e. the

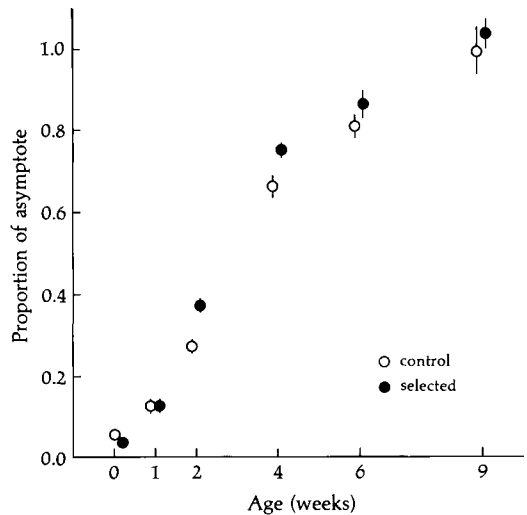


Fig. 1. Relationship between lipid-free mass and age in control and selected lines of Japanese Quail. Mass is scaled according to the asymptote of the Gompertz equation fitted to each line.

point of maximum rate of absolute mass increase. Asymptotes of each of the components of the P line were 2.10–2.14 times those of the C line (Table 2). There was less difference between lines and less consistency among components in growth-rate constants. The values of *K* for the fresh and lean masses of the P line exceeded those for the C line by 28% and 26%. These are lower than the ratios obtained by Marks (1978a, 1.47 for males and 1.35 for females), but the results are not strictly comparable because Marks used logistic equations and included measurements of masses of individuals repeated at weekly intervals from 2 through 8 weeks as well as subsample means for ages 0 and 1 week.

Compared to the ratios between lines in values of *K* for wet and lean masses, the water contents of the P chicks appeared to increase relatively more rapidly (ratio of *K*-values, 1.45), and the growth rates of the dry, extracted masses did not differ significantly. These discrepancies are difficult to interpret because small changes in mass early in the growth period can have a large effect on the value of *K*. The lean masses of chicks of the two lines normalized by their asymptotes are compared in Fig. 1. As we shall demonstrate in greater detail below, the divergence in the *K*-values between the lines is associated primarily with differ-

TABLE 3. Increase in constituents of Japanese Quail chicks during the growth period. Data are expressed as proportions of 9-week values.<sup>a</sup>

Age (weeks)	Sample		Wet mass		Increment		Lean wet mass		Increment		Lean		Increment		Lipid <sup>b</sup>		Increase <sup>b</sup>	
	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P
0	6	3	0.05	0.03	—	—	0.06	0.03	—	—	0.04	0.02	—	—	0.00	0.00	—	—
1	7	6	0.13	0.12	2.43	3.87	0.14	0.14	2.47	3.97	0.12	0.12	3.05	5.00	0.01	0.01	0.002	0.003
2	6	5	0.27	0.31	2.11	2.98	0.30	0.40	2.12	2.93	0.27	0.34	2.30	2.98	0.01	0.02	0.005	0.014
4	6	4	0.65	0.72	2.38	2.02	0.71	0.75	2.34	1.90	0.72	0.71	2.61	2.06	0.04	0.09	0.026	0.070
6	6	4	0.81	0.83	1.25	1.15	0.80	0.78	1.13	1.04	0.86	0.80	1.19	1.13	0.13	0.19	0.093	0.098
9	4	4	1.00	1.00	1.23	1.20	1.00	1.00	1.25	1.28	1.00	1.00	1.17	1.25	0.15	0.16	0.018	-0.025

<sup>a</sup> Nine-week values were: wet, C = 127.2, P = 282.3; lean wet, C = 110.8, P = 242.8; lean, C = 33.3, P = 72.3. Standard errors of the means were mostly less than 5%.

<sup>b</sup> Values of lipid normalized by the wet mass at each age, rather than the 9-week value. Increases are increments in the normalized value.

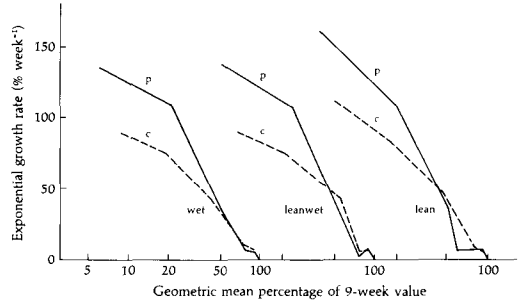


Fig. 2. Exponential growth rates (%/week) of Japanese Quail as a function of body mass for fresh, lipid-free, and lean components. The mass for each period of growth is the geometric mean of the initial and final values and is plotted on a logarithmic scale.

ences in rates of growth during the first 2 weeks after hatching.

The relative masses of the various components at each sample age and the relative rates of increase in mass during each interval between samples are shown in Table 3. For each component, rates of increase in the P line exceeded those of the C line only during the first two intervals (0-1 week and 1-2 weeks). In addition, the relative amount of fat stored by P chicks increased markedly during the interval between 2 and 4 weeks, whereas rapid increase in fat did not occur in the C line until after the fourth week. By 9 weeks, lipid storage in the two lines was comparable (15% and 16% of the lean mass).

Comparisons of growth rate based on age intervals can show differences because the two lines do not maintain the same sizes relative to their final masses at each age interval. The fact that growth increments of the P line are typically less than those of the C line after the second week may reflect only that the P chicks are closer to their asymptotes at that age and that their relative growth rates have slowed accordingly. We compared growth rates during each age interval relative to the proportion of the asymptote achieved by chicks of each line. In Fig. 2 the exponential growth rate of the wet, lean, and extracted components during each age interval are plotted as a function of the percentage of the asymptote achieved for each line. Exponential growth rate (%/week) during the period *i* to *j* is calculated by the expression  $100 \times [\log M(j) - \log M(i)] / (j - i)$ . The percentage of the asymptote achieved during a

TABLE 4. Components of Japanese Quail chicks as average percentages of the total lipid-free wet mass (yolk excluded for age 0-weeks average).

Component	0 weeks		1 week		2 weeks		9 weeks	
	C	P	C	P	C	P	C	P
Body	24.80	26.42	24.38	24.98	22.48	25.25	29.28	25.79
Skin	9.70	9.85	6.12	5.87	6.07	6.55	4.91	4.60
Plumage	3.34	2.41	6.30	4.18	6.23	4.43	3.48	4.00
Head	14.32	16.41	8.54	5.87	6.05	4.27	3.41	2.77
Brain	3.46	3.42	1.38	0.79	1.02	0.31	0.39	0.18
Leg (total)	8.26	8.42	8.43	8.38	9.25	9.62	8.13	8.82
Leg muscle	3.55	3.85	5.12	5.23	5.80	6.56	5.93	6.69
Pectoral muscle	1.52	1.41	6.94	9.68	14.75	17.62	18.53	24.37
Wings	2.81	2.27	4.85	4.72	6.84	6.52	4.37	4.14
Heart	1.18	1.53	1.49	1.79	1.04	1.12	1.08	1.18
Liver	4.63	3.39	5.08	6.71	3.73	3.63	4.16	3.92
Stomach	9.20	9.26	8.02	7.96	5.55	4.41	3.59	3.05

particular interval is calculated as the geometric mean, i.e.  $[M(i) \times M(j)]^{0.5}$ , divided by the asymptote. Plotted in this fashion, the data show clearly that differences in the growth rates of the two lines are limited to the intervals 0-1 and 1-2 weeks. From the age of 2 weeks onward, the growth rates of chicks are indistinguishable statistically between the two lines. These data are in agreement with the observation that relative growth rates of selected P-line chicks were greater than those of non-selected C-line chicks only prior to 2 weeks (Marks 1978a).

*Body proportions.*—The allocation of mass among the various body components in the two lines is compared in Table 4. At hatching, body proportions in the two lines were generally similar. The largest discrepancies were in the plumage, wings, and liver, all of which were relatively heavier in the C line. These were balanced by somewhat larger head and body (carcass) components in the P line. At 1 and 2 weeks, the relative masses of the head and plumage components of C-line chicks were approximately 50% greater than those of P-line chicks. At 9 weeks, two striking differences were the relative sizes of the pectoral muscles (P 24%, C 19%) and the contrasting relative sizes of the head (P 2.8%, C 3.4%) and, especially, the brain (P 0.18%, C 0.39%)—though the brain was not particularly large in either line. Except for these components, the relative proportions of chicks of the two lines were similar throughout the course of development.

The relationship of mass-specific growth rate to proportion of asymptote achieved was sim-

ilar in most components to the pattern for the body as a whole. As an example, we plotted this relationship for the leg muscles (Fig. 3), where the early difference in growth rates between the lines is evident. In contrast, however, the brain grows comparatively slowly in both lines with no systematic difference between the two.

*Water content.*—Differences in precocity between species and differences in level of function between ages within the same species usually are associated with differences in the proportion of water in tissues. Water contents of components of chicks (Table 5) revealed only trivial differences, none significant, between lines. A difference in the timing of plumage development probably accounts for the observed differences in the water contents of the plumages. The results of this study do not indicate major differences between the lines in the acquisition of mature function by any of the major tissues, at least so far as one may judge by water content.

#### DISCUSSION

Our principal results may be summarized as follows: (1) Selection for 4-week body mass led to an increase of about 110% in the asymptote of fitted Gompertz growth equations, i.e. more than a doubling in mature size, and a 26-28% increase in growth-rate constant. (2) The lengths of most of the appendages also increased in association with the change in mass, although in less than the expected proportion of the cube root of mass in most cases. (3) The difference

in growth rates between the lines was expressed entirely during the first 2 weeks of growth, before the chicks had achieved 50% of mature mass. (4) Proportions of organs and other components of the chicks during the growth period did not differ between the two lines, except that the pectoral muscles of P-line chicks became relatively larger than those of control chicks and the heads and, especially, the brains of P-line chicks became relatively much smaller. In fact, the lines did not differ in the absolute growth of the brain, in contrast to all other tissues. (5) There were no differences between lines in the water contents of tissues of chicks of similar ages.

Selection for 4-week body mass has produced a remarkable increase in the mature mass of Japanese Quail and a lesser, although still quite significant, increase in the rate at which mature mass is achieved. In the context of a three-parameter sigmoid growth model, such as the Gompertz equation, mass at a particular age can be increased by increasing the value of either the asymptote ( $A$ ), growth-rate constant ( $K$ ), or mass at age 0 (which is equivalent to reducing the age at the inflection point). Because selection on the P line was applied at age 4 weeks, when chicks of the control line have achieved about two-thirds of their mature mass, it is not surprising that  $A$  should predominate in response. Figure 2 shows quite clearly, however, that the increase in  $A$  resulted primarily from increases in growth rate during the first third of the growth curve, i.e. before the age of 4 weeks. Hence selection has not produced a simple change in one or both of the parameters  $A$  and  $K$  of the Gompertz equation (Ricklefs 1985). Apparently, growth rates during different periods of postnatal growth are, at least in part, genetically independent (see Kinney 1969). Thus the shape of the growth curve was altered by selection, as well (see Abplanalp et al. 1963).

Although the constants of fitted equations do not provide the best means for comparing growth rates when the shapes of the growth curves differ, differences in the magnitude of  $K$  between the P and C lines were roughly similar to differences in the mass-specific growth rates during the earlier part of the growth period. The increase of almost 30% in  $K$  in the selected line, though substantial, is not large compared to the difference between altricial and precocial species of similar adult size. When

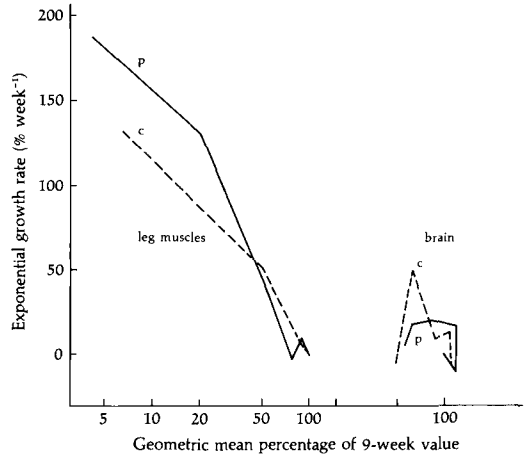


Fig. 3. Exponential growth rates of the lipid-free components of leg muscles and brains of selected and control lines of Japanese Quail. Data are plotted as in Fig. 2.

growth rates of species are adjusted for adult size by calculating the residuals from a regression of the log of  $K$  against the log of  $A$  or adult mass, altricial and precocial species are separated by about  $0.5 \log_{10}$  units, a factor of 3.2. The 1.3 factor by which the P and C lines differ is equivalent to about  $0.1 \log_{10}$  units. Hence the scale of selective change that we are considering here is on the order of variation within taxonomic families of birds having rather similar patterns of development, rather than between groups of species with different modes of development. It will be instructive, nonetheless, to determine the degree to which changes in growth rate and pattern of development in selected quail correspond to the predictions of hypotheses to explain variation in growth rates of birds more generally.

One hypothesis concerning the diversification of growth rates suggests that growth rate is evolutionarily flexible independently of other aspects of morphology and physiology, and that the observed rate is optimized with respect to such ecological factors as predation and food availability. According to this hypothesis, growth rate should be capable of adjustment without any basic reorganization of the body plan or pattern of development. The results obtained in this study are generally consistent with this hypothesis. Except for the brain (discussed below), no general changes in body proportions or in water contents of tissues were

TABLE 5. Percentages of water in components of Japanese Quail chicks.

Component	0 weeks		1 week		2 weeks		9 weeks	
	C	P	C	P	C	P	C	P
Body	81.2	81.9	77.3	76.5	74.6	76.0	72.5	73.2
Skin	82.4	79.8	72.0	69.2	75.9	77.3	68.6	69.2
Plumage	31.3	35.3	53.2	46.9	40.4	47.8	23.0	19.2
Head	83.9	85.2	80.1	77.9	78.2	78.5	68.0	68.5
Brain	87.8	87.9	85.0	84.7	85.4	87.8	83.4	84.5
Leg (total)	78.3	80.1	72.6	70.3	72.9	73.0	67.9	68.2
Leg muscle	82.6	81.6	78.3	76.1	77.8	78.3	76.4	76.7
Pectoral muscle	88.7	89.5	78.3	78.1	75.3	74.7	73.8	74.1
Wing	84.2	83.5	73.2	71.4	70.5	71.0	61.0	62.5
Heart	84.9	84.7	79.1	80.0	78.4	79.5	77.2	77.7
Liver	80.3	81.6	76.9	77.6	75.6	76.3	74.2	75.6
Stomach	77.9	79.2	74.7	75.5	75.5	76.3	73.9	75.0

observed. The responses of particular organs to selection did vary, however. That of the pectoral muscles was greatest, and the relative mass of these muscles increased as a result of selection for 4-week body mass.

In marked contrast to other components, there was no response in the growth rate of the brain, so that relative brain size decreased considerably in selected lines (Ricklefs and Marks 1984). Evidently, the lack of response did not preclude a general response in the body as a whole. In addition, the general response probably did not depend in any way on the observed increase in the relative size of the pectoral muscles. On the contrary, the larger growth increment of the pectoral muscles (mature/neonate) would seem to dictate a longer growth period and hence a slower growth rate overall, all other things being equal. The pronounced response of the pectoral muscles, without apparent change in the proportion of water in the tissue or other quality (Fowler et al. 1980), further supports the hypothesis that growth rate can be increased, at least in the amount observed in selected quail, without basic reorganization.

The general lack of change in water contents and relative sizes of most components of quail following selection for body size weighs against two other hypotheses. One proposes that growth rate can be increased only in conjunction with such changes in the visceral organs as make available larger quantities of energy or nutrients to fulfill increased requirements. We did not observe any differences in the relative proportions or water contents of visceral organs between selected and control lines at the

ages sampled. That nutritional quality of the diet is an important consideration for growth rate has been illustrated by the poor early mass gains of P-line chicks when reared on a low protein (20%) diet (Marks 1978a). With a diet of adequate quality, however, the visceral proportions of unselected quail appear to be adequate to supply the needs of more rapid growth. Energy requirement *per se* does not increase in direct proportion to growth rate because metabolic costs of maintenance also are included in the total. One presumes that biosynthesis of structural components does increase in direct relation to rate of growth. And while much synthesis occurs in the growing tissues themselves, such growth must be supported ultimately by the organs of digestion, assimilation, and biochemical transformation.

Experimental force-feeding of young chicks of the domestic fowl results primarily in an increase in lipid deposition and a relative increase in the visceral organs, and rates of food intake do not increase until a week or more after the beginning of such experiments (Nir et al. 1974, 1978). These results suggest that *ad libitum* (i.e. control) food intake is near the maximum possible, but that growth rate (in the sense of  $K$  of a sigmoid equation) does not increase even after hypertrophy of the visceral organs leads to an increase in total rate of food consumption. One of the difficulties with the experiments of Nir et al. (1974, 1978) is that, to force-feed the chicks, the food was mixed with water to form a slurry that could be introduced to the proventriculus by a tube. Hence the response of the digestive system might have been to handling a more aqueous diet.



Experiments with mild cold stress of chicks of the domestic fowl have shown that metabolizable energy can be increased voluntarily by increasing food consumption in response to the increased demands of temperature regulation, but the responses usually are not completely compensating (Kleiber and Dougherty 1934, Osbaldiston 1966). On balance, it seems unlikely that rate of assimilation is apt to place an upper bound on realizable growth rate.

A second hypothesis based on internal limitation of growth rate suggests that the rate at which tissues can grow is limited by cellular processes of replication and biosynthesis. Hence the maximum growth rate is determined not only by characteristics of embryonic cells, but also by the proportions of tissues that are composed of embryonic cells at each point of development. Ricklefs (1979a, b) has shown that these ideas are consistent with the approximately four-fold difference in growth rate between altricial and precocial species and with the gradual decline in mass-specific growth rate observed over the course of development in all species. As a general rule of thumb, the relative proportions of embryonic and differentiated (i.e. mature) cells in a tissue, such as skeletal muscle, are directly related to the proportion of water. This is consistent with differences in water content between altricial and precocial birds during the early portions of the development period and with the gradual decline in water content of all tissues with growth. Ricklefs and Webb (1985) have further shown a direct relationship between water content and functional capacity of skeletal muscle in the European Starling (*Sturnus vulgaris*) as the tissue changes over the course of the growth period. In this study, however, we could find no systematic differences in the water contents of the tissues of selected and control lines of Japanese Quail. Thus, using water content as a criterion for functional maturity, there was no suggestion that the selected change in growth rate was accompanied by any change in the precocity of the chicks. It has been demonstrated, however, that muscle cation concentrations and electrical potential may change during development independently of water content (Draper 1968, Karzel 1968, Ranaweera and Wise 1982).

Ricklefs (1979a) also suggested that the growth rate of the individual as a whole could be increased by reducing the growth incre-

ment of any one tissue whose rate of growth constrained that of the whole. That is, in order to maintain body proportions within certain limits during the growth period, each tissue, regardless of its inherent potential, can grow no faster than the most slowly growing tissue. By *reducing* the growth increment of the limiting tissue, and thereby also changing body proportions in a particular way, the length of the growth period is reduced and the remainder of the body is allowed to grow more rapidly, i.e. to reduce the length of the growth period of the organism as a whole to a comparable degree. Again, we could find no evidence of reduced absolute size of any component in the P line to support this possibility. Ricklefs (1979a) suggested that the leg muscle might constrain growth rate in birds, but the growth increment of the leg muscle in the P line greatly exceeded that in the C line.

We had no reason to believe that pectoral muscles might be such a limiting tissue, and their growth increment was observed to increase following selection, not decrease as predicted by the hypothesis. The relative size of the brain of selected quail was much smaller than that of controls, but the growth increments of the brain did not differ between the two lines. Hence we found no evidence of a change that might have reduced the development period of the brain, although this may have been brought about in some other way not yet appreciated. The response of the brain component did, however, emphasize that the individual components of the organism may respond to selection independently, in contrast to a view that growth rate is controlled by a single factor that affects all tissues to the same degree.

Finally, apparent changes in growth rates could be caused by a shift in the timing of development of one or a small number of components, especially the development of the plumage. Although the relative mass of the plumage of C-line chicks was greater than that of P-line chicks during the early development period, this difference would have increased the apparent growth rate of the C-line chicks relative to P-line chicks, rather than vice versa as observed. Moreover, the growth rates of all components except the brain increased in response to selection, and so regardless of any changes in body proportions at least part of the response to selection resulted from a general

increase in growth rate among all tissues. It would appear that the basic time scale of development was altered.

It is difficult to determine whether we can extrapolate the results of this study to the broader variation of growth rates among birds more generally. Although differences between the P and C lines do not correspond to the set of traits, i.e. growth rate and precocity of development, that distinguish altricial and precocial birds, they may be fully representative of the variation within narrower taxonomic groups. Moreover, developmental differences between altricial and precocial birds may not be relevant to the differences in their growth rates. The response of the P-line chicks was, however, peculiar, at least in the lack of response of the brain, which resulted in highly atypical proportions for galliform birds (Ricklefs and Marks 1984). Conceivably, extremely strong artificial selection could bring about a response in growth rate accomplished by mechanisms that would reduce fitness in the more complex natural environment. If this were true, the results reported here might have no bearing whatsoever on the differences in growth rates observed among species in nature.

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