# Heritabilities of growth curve parameters and age-specific expression of genetic variation under two different feeding regimes in Japanese quail (*Coturnix coturnix japonica*)

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## Summary

This study investigated genetic variation in growth and final size in relationship to differences in heritabilities under good and poor feeding conditions. Heritabilities of growth and final size were estimated for several traits under *ad libitum* and restricted feeding conditions. A 30 % feed restriction from hatching to 44 days of age in Japanese quail chicks decreased body weight and tarsus length at 44 days of age and the length of the third primary covert feather at 24 days of age relative to controls fed *ad libitum*. Wing length at 44 days of age was not significantly different for *ad libitum* fed and restricted quail. Genetic variances for body weight and tarsus length were very large throughout growth which resulted in heritability estimates close to one for these traits. The genetic correlations among feeding treatments were low, indicating that different genes were affecting growth under the two treatments. Growth was described by the components: asymptote, growth period, and shape of the growth curve following the modified Richards growth curve model (Brisbin *et al.* 1986). Tarsus length, which had high heritability of the parameter 'growth period' of the model, tended to display a higher heritability under the restriction than under *ad libitum* feeding. Body weight and feather length, which had either no heritable or low heritable 'growth periods' estimates, tended to be more heritable under *ad libitum* feeding. The shape parameter of the growth curve was not heritable for any trait, except tarsus length under restricted feeding.

## 1. Introduction

Variation in heritability estimates and dissimilar responses to selection under different environments have long been a major concern in quantitative genetics (e.g. Falconer, 1952, 1960, 1990; Robertson, 1964; Sørensen, 1985). The objective of this work was to determine optimum feeding conditions to achieve maximum responses to selection in animal breeding (e.g. Marks, 1978; Nielsen & Andersen, 1987; Park *et al.* 1966). Recently, studies involving natural populations have shown that heritabilities of ecologically important traits are not static properties of these populations, but vary according to the current environmental conditions (review in Parsons, 1987; van Noordwijk *et al.* 1988; Gebhardt-Henrich & van Noordwijk, 1991). The relationship between the expression of genetic variation and different environ-mental conditions influences the response of populations to natural selection.

The direction of change in heritabilities under unfavourable conditions is not clear. Examples exist when a stressful environment led to a greater response to artificial selection (Parker & Bhatti, 1982; Sørensen, 1977) and vice versa (Sørensen, 1985; Marks, 1978; Nielsen & Andersen, 1987). Simulations with growth rates and asymptotes have shown that the amounts of heritable variation in the asymptote of the growth curve, and the length of the growing period influence the heritability of the fully grown trait under good and poor environments (Gebhardt-Henrich, 1992).

The objectives of the following study were to measure the heritability of growth curve parameters for several traits, e.g. asymptote, length of the growth period, and the shape of the growth curve, and to determine the relationships of these estimates with heritabilities of the fully grown traits under both *ad libitum* and restricted feeding regimes. Growth curve analyses require a mass of data during the growing period and the measurements themselves may disturb

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Table 1. *Experimental setup of the half-sib breeding design which is explained in detail in the text*

| Set | Males | Females | Chicks |
|---|---|---|---|
| 1 | 1 | 1 | 6 chicks to 3 control decks<br>6 chicks to 3 restricted decks |
| | | 2 | 6 chicks to 3 control decks<br>6 chicks to 3 restricted decks |
| | 2 | 3 | See above |
| | | 4 | See above |
| | . | . | |
| | 10 | 20 | |
| 2 | 11 | 21 | |
| | . | . | |
| | . | . | |
| | 20 | 40 | |

the growth of e.g. free-living birds (Zach, 1988). Therefore, the Japanese Quail as a laboratory animal was chosen and measurements were taken on body weight, length of the metatarsus (referred to as tarsus length), length of the third primary covert feather, and wing length. Whereas body weight and tarsus length are good representatives of overall body size in birds, ulna (wing bone) length and wing length diverge significantly from multivariate measures of overall size in birds (Garnett, 1976; Rising & Somers, 1989). Body weight is also a measure of condition and is likely to be affected by feeding regimes. The growth of the third primary covert feather is very short, this feather is not present before 2–3 days after hatching and reaches its final length before 3 weeks after hatching. Thus, these traits can be expected to have different growth trajectories and can be used to test the relationship between the expression of genetic variation during growth with the final sizes of these traits.

## 2. Materials and Methods

### (i) *Experimental design*

Quail utilized in this study were from a randomly mated control population (Marks & Lepore, 1968). A half-sib breeding design was carried out as follows (Table 1): 80 females in individual cages were mated to 20 males (4 females per male) by switching males between cages daily. Eggs were collected for 3 weeks and stored in a chilled room at 10 °C until set to allow two hatches 3 days apart. This was necessary due to time limitations for data collection. At hatching, only chicks from 2 females, of the 4 per sire, that produced at least 12 chicks were utilized. On hatching day the 12 chicks from each of 20 females (mated to the first 10 males, set 1 in Table 1) were randomly placed into 6 decks, 2 chicks from each female per deck. Eggs from 20 other females (mated to a second group of 10

males, set 2 in Table 1) were hatched 3 days later and their chicks were distributed to another 6 decks as described in set 1 above. Control treatment chicks were placed in alternate decks and had access to high protein food (28 %, see Marks & Lepore, 1968) *ad libitum* throughout growth with food intake measured daily. Chicks in the other decks received 70 % of the food amount that *ad libitum* chicks had consumed during the preceding day. Water was available to all chicks at all times.

Chicks were sexed when they were 3 weeks-old and rechecked when they were 4 weeks-old by their plumage colouration.

Chicks were weighed individually on day 0 (= hatching day), day 1, day 2 and then every other day until day 44. Tarsus length and the length of the third primary covert feather were measured using callipers every 2 days, wing length was measured as the flattened wing on measuring grid paper every two days. The third primary covert feather was measured until the chicks reached 24 days of age, because its growth ceased before then. All other traits were measured until chicks reached 44 days of age. All measurements were made by the first author.

Growth data were fitted to a modified Richard curve (Brisbin *et al.* 1986):

$$\frac{W_{i+1} - W_i}{t_{i+1} - t_i} = \frac{2(m+1)}{T(1-m)}(A^{1-m}W_i^m - W_i) + e_i,$$

where $W_i$ is the body size measurement at time $t_i$, $A$ is the asymptotic measurement, $T$ is the overall growing time and is called growth period, $m$ is the shape parameter.

A stochastic error at time $i$ ($e_i$) is incorporated in this model (White & Brisbin, 1980). This model takes autocorrelation of successive data points from the same individual into account and all three parameters ($A, m, T$) are free to vary independently from each other (White & Brisbin, 1980). The asymptote represents the size of the bird that is approached during growth, the $T$-parameter is a measure of growth rate and is given as the number of days required for the entire growth process and $m$ indicates the shape of the growth trajectory (Brisbin *et al.* 1986). An increase in the shape parameter ($m$) means that the part of the curve of linear growth is steeper (i.e. maximum growth rate is higher) and the inflexion point (point where accelerating growth turns into the decelerating phase) is later. An illustration and further details are provided in Brisbin *et al.* (1987) and references therein. The parameters $A$, $T$, and $m$ were estimated using the SAS NLIN Procedure (SAS Institute, 1988). Additionally, data were analysed using a modification of the estimation procedure to better estimate the $m$-parameter (McCallum & Dixon, in press). The method with the better fit was then chosen.

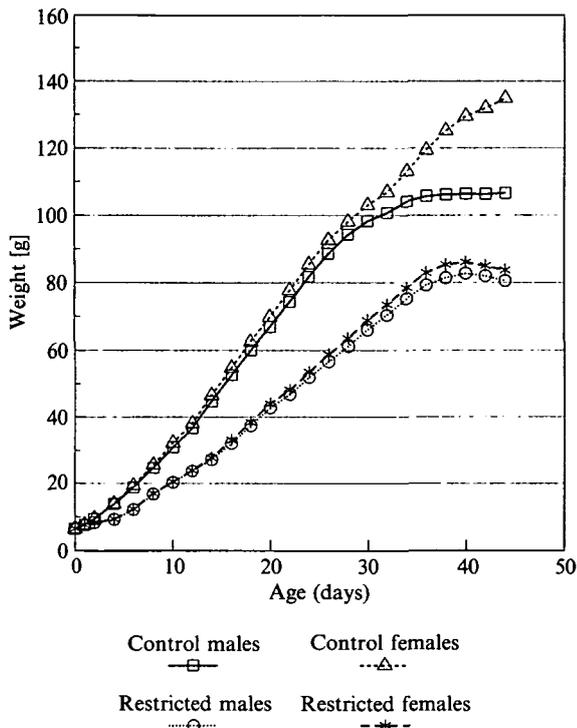Tarsus length and wing length of the parental birds were also measured. Due to different age, however,

Fig. 1. Growth curves based on body weight [g] in *ad libitum* fed (control) quail chicks and for 30% feed restricted chicks.

their body weights could not be considered the same trait as their offsprings' weights. It was not possible to measure the length of the third primary covert feather in the parental birds because of feather damage.

### (ii) *Statistical analysis*

Variances of body weight and tarsus length were strongly positively correlated with the mean, a well-known phenomenon (Atchley, 1984). Therefore, body weight and tarsus length were log-transformed to eliminate the association between means and variances. Measurements of the 3rd primary covert feather and wing length did not need transformation.

The traits (including the estimates of the growth curve parameters *A*, *T*, *m*) were checked for normality and homoscedasticity prior to the statistical analyses. If necessary, log 10 or reciprocal transformations were used. In cases where the estimation procedure led to unrealistically high or low values of the parameters, they were deleted.

Variance components were estimated by using Restricted Maximum Likelihood (REML) in the VARCOMP procedure of SAS (SAS Institute, 1988). In a few cases maximum likelihood and the general linear model were used additionally. If variance components could not be estimated by restricted maximum likelihood or maximum likelihood, the values were reported as missing in the tables. As indicated in the literature (Harville, 1977; Shaw, 1987) estimates from the restricted maximum likelihood were slightly higher, because the maximum likelihood estimator is biased downwards. The precision of the heritability estimates is higher with REML than with the General Linear Model (Henderson's Method) (Beaumont, 1991).

The following quantitative genetic model was assumed:

$$V_P = V_A + V_{EC} + V_{Ei},$$

where

$V_P$ = total phenotypic variance,

$V_A$ = additive genetic variance,

$V_{EC}$ = environmental variance due to pre-hatching maternal effects,

$V_{Ei}$ = individual environmental variance.

These causal components were estimated and the narrow sense heritability was calculated (Falconer, 1981, p. 170, f). The variance component due to deck was estimated, but not added to $V_P$, because it arose solely due to the experimental design (Atchley & Rutledge, 1980). This component was very small in all analyses. The standard error of the heritability estimate was calculated using the asymptotic co-

Table 2. *Final measurements of weight* [g], *tarsus length* [mm], *length of the third primary covert feather* [mm], *and wing length* [cm]. *These measurements were taken when the quail were 44 days old* (*or 24 days for the third primary covert feather*). *Quail chicks were fed either* ad libitum *or were 30% restricted from hatching day until the final measurements.*

| | Ad libitum | | Restricted | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| Weight | 106·5 (4·7)[a] | 134·5 (5·4)[b] | 80·8 (5·3)[c] | 84·4 (7·5)[c] |
| Tarsus | 28·54 (0·7)[a] | 28·91 (0·7)[a] | 28·15 (0·8)[b] | 28·45 (0·9)[ab] |
| Feather | 20·54 (0·6)[a] | 20·95 (0·5)[b] | 19·88 (0·7)[c] | 20·37 (0·9)[c] |
| Wing | 7·2 (0·2)[a] | 7·3 (0·1)[b] | 7·1 (0·1)[a] | 7·2 (0·2)[ab] |

Different letters indicate $P < 0.05$. Standard deviations are given in parentheses.
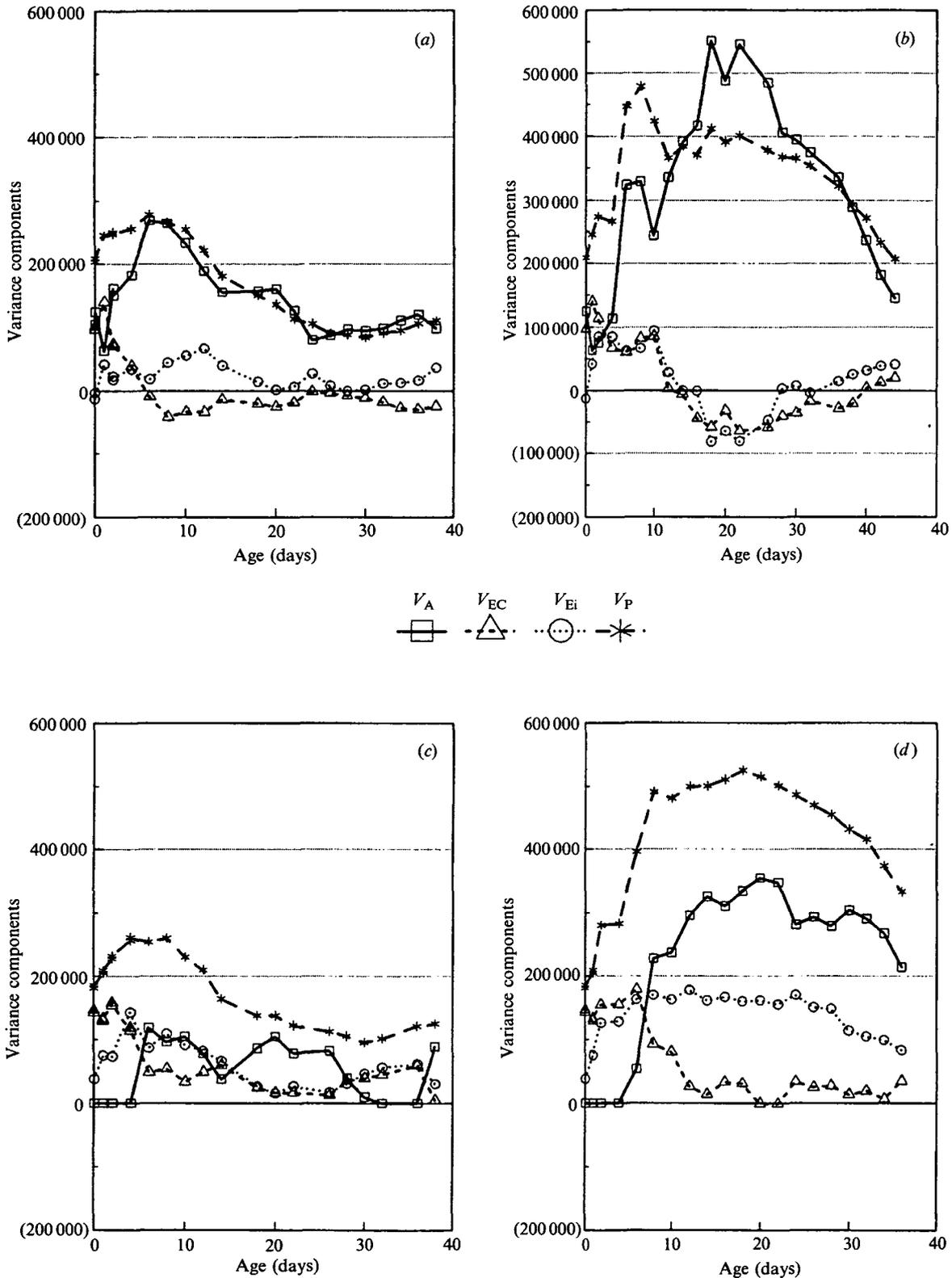The unit is the mean of a half-sib family, N = 20

Fig. 2. Variance components of log-transformed body weights throughout growth of quail chicks. $V_A$, additive genetic variance; $V_{EC}$, variance components due to pre-hatching maternal effects; $V_{Ei}$, individual environmental variance. (a) *Ad libitum* fed males, (b) restricted males, (c) *Ad libitum* fed females, (d) restricted females.

variance matrix of the estimate given by the REML procedure and the delta method (Bulmer, 1985, p. 86).

For tarsus length and wing length heritability estimates obtained from parent–offspring regression were combined with the estimates from the half-sib analyses. For the parent–offspring regressions the mean of the offspring was regressed on (sire + mean of the two dams)/2 and pooled with the regression of the mean of the offspring on their dam (Hill & Nicholas, 1974). The estimates from half-sib analyses and

Table 3. *Estimates of growth curve parameters from the modified Richards growth model of the traits body weight, tarsus length, and length of the third primary feather. Only body weights of male quail chicks were used. Curve parameters were separately calculated for* ad libitum *fed and restricted chicks. The asymptotic 95% confidence intervals are shown in brackets. A – asymptote, m – shape of the growth curve, T – growth period*

| Parameter | *Ad libitum* | Restricted |
|---|---|---|
| Weight A [g] | 109·64 (106·51–112·77) | 84·34 (79·67–89·00) |
| Weight m | 1·56 (1·21–1·91) | 2·29 (1·27–3·31) |
| Weight T [d] | 39·55 (36·13–42·98) | 46·09 (38·82–53·36) |
| Tarsus A [mm] | 29·54 (29·44–29·65) | 29·50 (29·32–29·67) |
| Tarsus m | 3·16 (2·86–3·47) | 3·24 (2·87–3·62) |
| Tarsus T [d] | 58·53 (56·85–60·21) | 84·36 (81·89–86·84) |
| Feather A [mm] | 21·02 (20·96–21·09) | 20·65 (20·60–20·70) |
| Feather m | 1·40 (1·32–1·48) | 1·37 (1·27–1·46) |
| Feather T [d] | 13·40 (13·19–13·62) | 15·93 (15·62–16·23) |

parent–offspring regressions were then combined following Hill & Nicholas (1974).

## 3. Results

### (i) *Weight*

Growth curves based on body weight for both sexes and both treatments are shown in Figure 1. Whereas weight gains of males and females were similar under restricted food conditions, weights for females increased more rapidly than weights for males under *ad libitum* feeding after 34 days of age.

Body weights of *ad libitum* fed males and females differed significantly between treatments at 44 days of age (Table 2). *Ad libitum* fed females were significantly heavier than *ad libitum* fed males (Wilcoxon $Z = -5·40$, $P < 0·0001$), but under restricted feeding conditions the body weight difference between males and females was not significant (Wilcoxon, $Z = -1·37$, $P = 0·172$). *Ad libitum* fed males were significantly heavier than restricted males (Table 2, $N = 20$ half-sib families, $F = 245·7$, $P < 0·0001$). *Ad libitum* fed females were also significantly heavier than restricted females ($N = 20$, Wilcoxon $Z = 5·40$, $P < 0·0001$).

Variance components during growth are shown in Figure 2 *a–d*. Except at the beginning, phenotypic variance consisted basically only of additive genetic variances in *ad libitum* and restricted males (Fig. 2 *a*, *b*). Hence heritability estimates were high throughout growth. They were lowest at hatching day $(0·60 \pm 0·03)$ and one day after hatching and often approached one thereafter. For female birds $V_{\mathrm{Ei}}$ was present throughout growth, resulting in lower heritabilities. At later ages, after the onset of laying in a few *ad libitum* fed females, heritability estimates were higher for restricted females, which had not started laying. Variances due to maternal effects before hatching were only present early. Variance components due to individual environmental effects were small throughout growth.

When variance components were estimated by maximum likelihood (ML) and restricted maximum likelihood (REML), estimates obtained by the latter method were higher (males: $h^2_{\mathrm{day}\,0} = 0·52$ for ML and $0·60$ for REML, $h^2_{\mathrm{day}\,4} = 0·35$ for ML and $0·43$ for REML). Variances were about twice as high in restricted birds as in *ad libitum* fed birds of both sexes. Genetic correlations based on sire averages between the *ad libitum* and the restricted food condition were naturally almost one on day of hatch, but decreased steadily after day 10 until they reached about 0·4 at day 44.

Table 4. *Heritabilities of the final measurements of growth under* ad libitum *feeding* $(= h^2_{\mathrm{ctrl}})$ *and restricted feeding* $(= h^2_{\mathrm{rest}})$ *and of the growth curve parameters of the modified Richards curve for body weight, tarsus length and length of the third primary covert feather*

| Trait | Final measurement | A | m | T |
|---|---|---|---|---|
| **Weight** | | | | |
| Control | 0·96 ± 0·02 | 0·75 ± 0·18 | 0·10, NS | 0·22, NS |
| Restricted | 0·70 ± 0·03 | 0·45 ± 0·25 | 0·00 | 0·15, NS |
| **Tarsus** | | | | |
| Control | 0·75 ± 0·13 | 0·53 ± 0·25 | 0·14, NS | 0·44 ± 0·19 |
| Restricted | 0·88 ± 0·14 | 1·26 ± 0·24 | 0·36 ± 0·14 | 0·57 ± 0·16 |
| **Feather** | | | | |
| Control | 0·53 ± 0·19 | 0·54 ± 0·19 | 0·20, NS | 0.01, NS |
| Restricted | 0·59 ± 0·19 | 0·36 ± 0·16 | 0·00 | 0·26, NS |
| **Wing** | | | | |
| Control | 0·32 ± 0·11 | Not estimated | Not estimated | Not estimated |
| Restricted | 0·49 ± 0·11 | Not estimated | Not estimated | Not estimated |

4

Control males     Control females
—☐—         ···△··

Restricted males  Restricted females
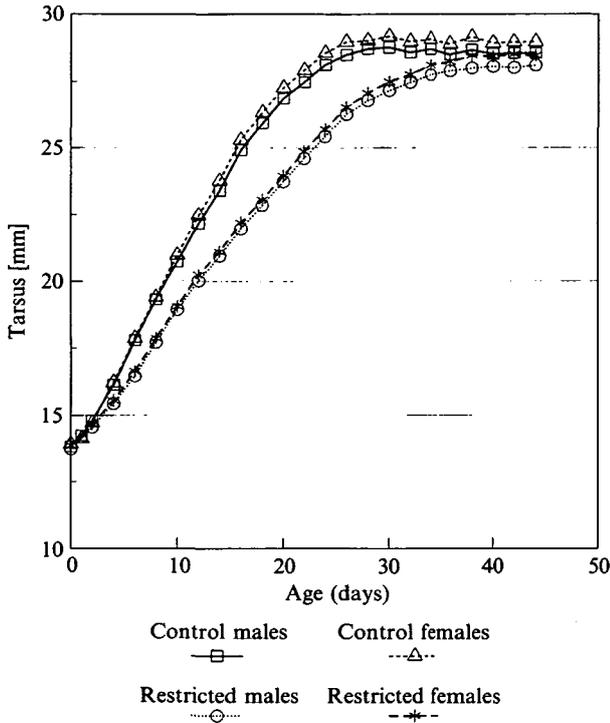····⊙····        – ✳ –

Fig. 3. Growth curves based on tarsus length [mm] for *ad libitum* fed quail chicks (control) and for 30% restricted chicks.

The modified Richards curve explained 98·4% of the variance of weight gain in control males and 93·8% in restricted males. The residuals were normally distributed and, when plotted against age, showed no pattern. This was true for all traits. The fit of the sigmoid growth curve was poorest for birds under restricted feeding. The growth of *ad libitum* fed

females was complicated by the secondary weight gain during sexual maturation (Fig. 1). Therefore, their weights were not fitted to the sigmoid growth model. The growth curves for male weight had significantly higher asymptotes in the *ad libitum* treatment than in the restricted treatment (Table 3). The means of the $m$ and $T$ parameters were lower for *ad libitum* fed males than for restricted males, but the 95% confidence intervals of the estimates overlapped (Table 3). The heritability estimate for the asymptotes was higher for *ad libitum* fed males than for restricted males (Table 4), but the difference was not significant. The heritability estimates for the 44 day body weights in males were higher than that of the asymptotes (Table 4). The shape parameter '$m$' was not heritable for either treatment. The reciprocally transformed $T$-parameter indicating the length of the growth period was moderately heritable for both treatments (Table 4).

### (ii) *Tarsus*

Growth curves for tarsus length are shown in Figure 3. Females had longer tarsi than males under both treatments, however, since differences were not significant (Table 2), sexes were pooled for further analyses. Under restricted conditions males had significantly shorter tarsi than under *ad libitum* conditions, in females the difference between treatments was not significant.

Variance components for tarsus length are shown in Figure 4. Since there was no difference for males and females, sexes were combined. The environmental
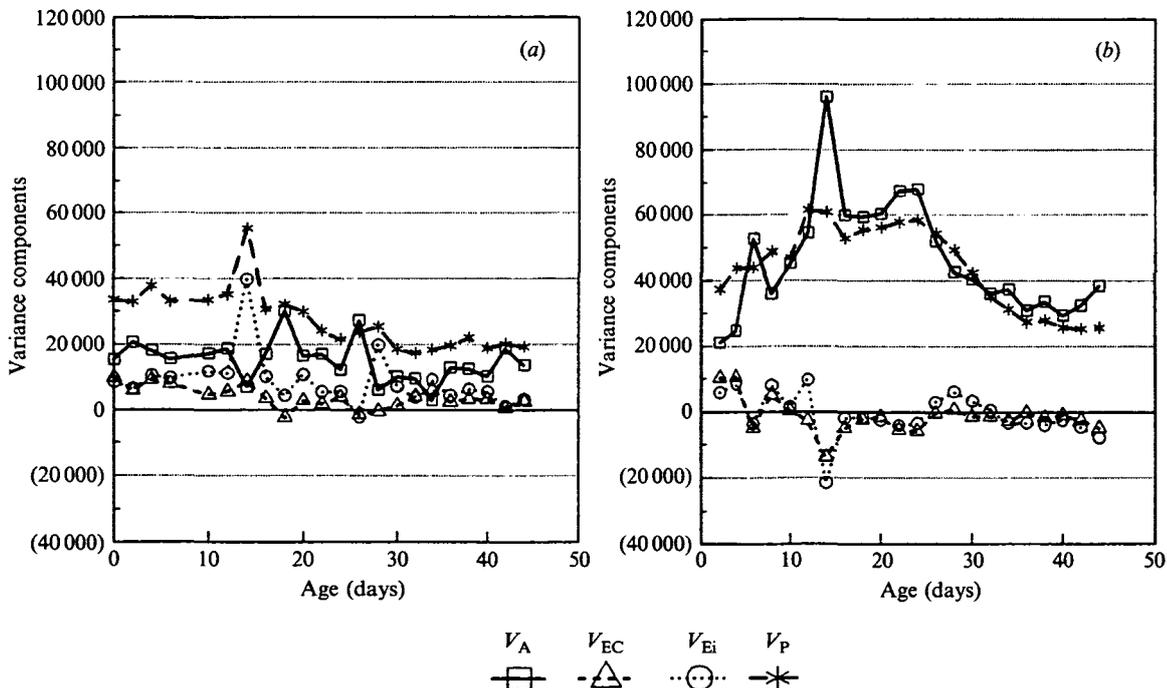


$V_A$    $V_{EC}$    $V_{Ei}$    $V_P$
—☐—  -△-  ··⊙··  —✳—

Fig. 4. Variance components of log-transformed tarsus lengths throughout growth. (*a*) *Ad libitum* fed chicks, (*b*) 30% restricted chicks. For further symbols see Figure 2.
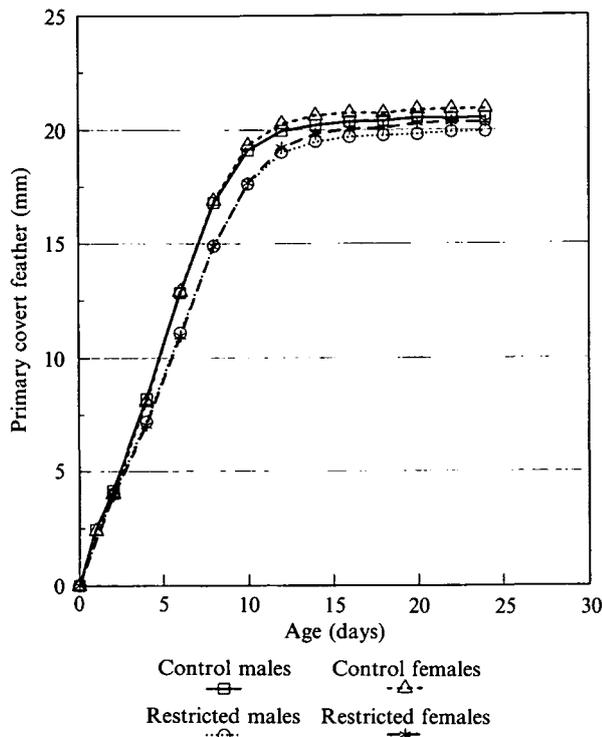
Fig. 5. Growth curves of the third primary covert feather [mm] of *ad libitum* fed chicks (control) and 30% restricted chicks.

variance components generally made some contribution to $V_P$ in *ad libitum* fed birds. In restricted birds $V_{EC}$ and $V_{Ei}$ were close to zero throughout growth and $V_A$ was of the same magnitude as $V_P$.
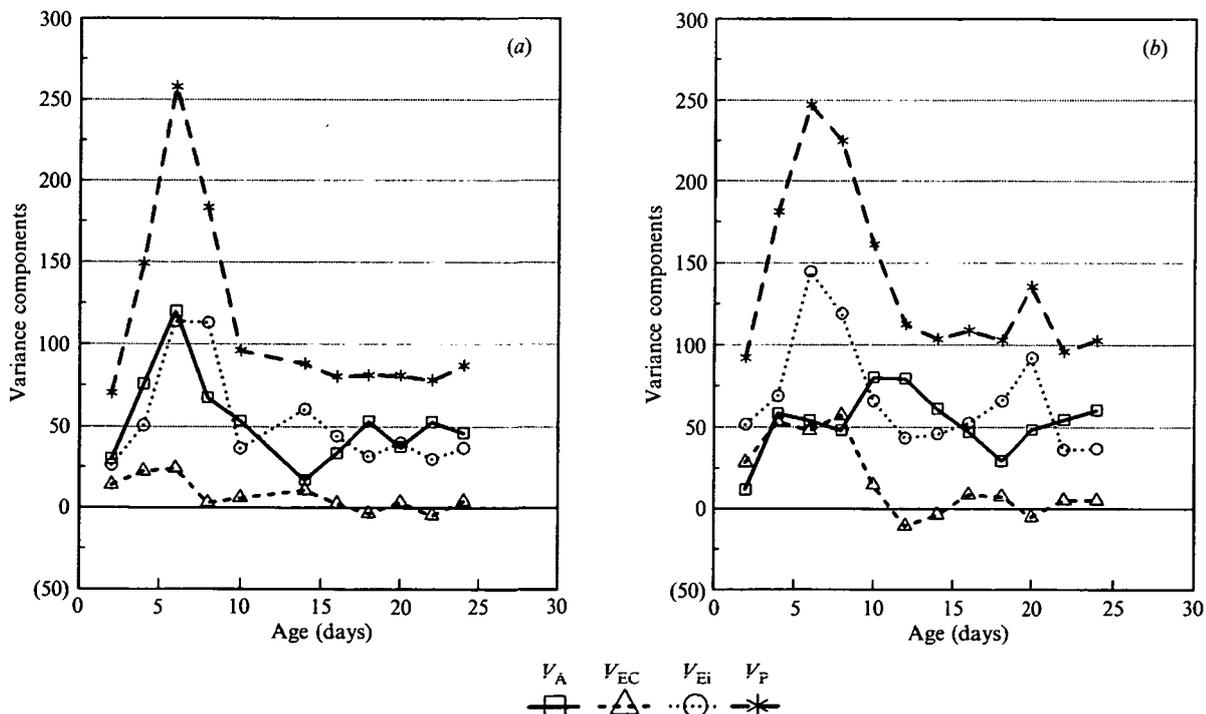
Because final tarsus length was almost unaffected by food restriction, the combined heritability estimate of tarsus length from parent-offspring regression and half-sib analyses was not significantly different for birds in either treatment (Table 4). Since this pattern was similar for both sexes, they were pooled. Heritability estimates from half-sib analyses were within the 95% confidence interval of the estimate from parent-offspring regression.

The modified Richards curve explained 97·5% of the variation in tarsus growth in *ad libitum* fed and 96·3% in restricted quail. The asymptote and the shape parameters of the growth model were very similar for birds of both treatments, but the growth period was much longer for restricted birds (Table 3). The heritability of the asymptote of restricted birds was about twice as high as the heritability of the asymptote of *ad libitum* fed birds (Table 4). The other two curve parameters, the log-transformed *m*-parameter and the *T*-parameter also showed higher heritabilities in restricted birds, but the difference was not significant for either parameter (Table 4).

(iii) *Third primary covert feather*

The third primary covert feather grew very rapidly. It was not present on day of hatch and reached its final size on the 20th day under *ad libitum* feeding conditions and about 4 days later under restricted feeding conditions (Figure 5). Females had significantly longer primary covert feathers than males under *ad libitum* feeding conditions ($F = 5·46$, $P = 0·025$, $N = 20$), but



Fig. 6. Variance components based on the length of the third primary covert feather throughout growth of *ad libitum* fed chicks (*a*) and 30% restricted chicks. (*b*) For symbols see Figure 2.
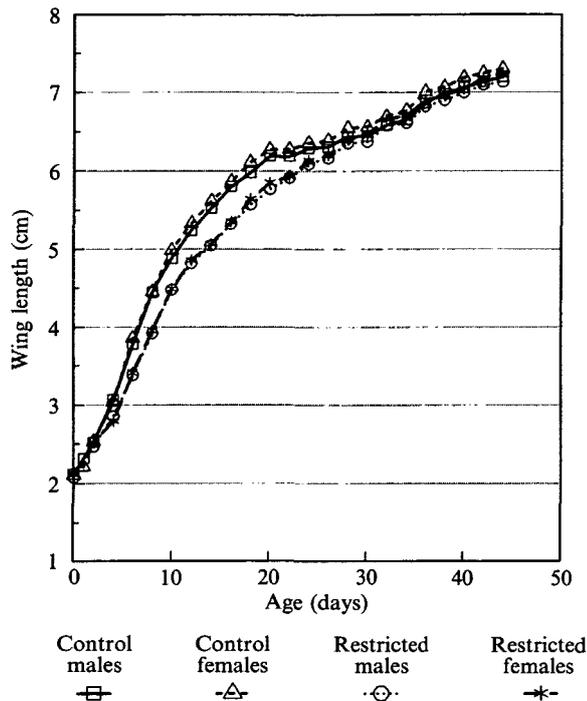
Fig. 7. Growth curves of wing length (cm) of *ad libitum* fed chicks (control) and 30% restricted chicks.

the sex difference was not significant under restricted feeding conditions (Table 2). Primary covert feathers of both sexes were significantly shorter under restricted feeding (males: Wilcoxon, $Z = 2.75$, $P = 0.006$, females: Wilcoxon, $Z = 2.12$, $P = 0.03$).

Phenotypic variances in both treatment groups peaked at day 6 and then fell to initial levels (Figure 6). Heritabilities were initially not significantly greater than zero, but became significant at around day 16 in *ad libitum* fed birds and day 20 in restricted birds. Heritability estimates for final length of this feather were similar for *ad libitum* fed and restricted birds (Table 4).

The modified Richards curve explained 99.9% of the variation in feather growth of *ad libitum* fed and 99.9% of restricted birds. The estimated asymptote of the third primary covert feather from the growth model was significantly lower in restricted quail and their growth period was significantly longer (Table 3). The heritability estimate of the asymptote for restricted birds was lower, but not significantly different from that of *ad libitum* fed birds (Table 4). It was very similar to the heritability of the final length of this feather. None of the heritability estimates of the other curve parameters for either treatment were significantly different from zero.

(iv) *Wing*

Growth curves of wing length are shown in Figure 7. Females had slightly longer wings under both treatments, but this difference was only significant under *ad libitum* feeding conditions (Table 2). Restricted

birds tended to have shorter wings than *ad libitum* fed birds; however, the differences were not significant (Table 2). Total phenotypic variances were higher in restricted birds during early growth, but similar to the *ad libitum* fed birds at later ages (Figure 8).

Heritabilities during growth and at the end of growth tended to be higher in restricted birds, although not significantly so. The heritability estimate of wing length from parent–offspring regression was $0.29 \pm 0.12$ for *ad libitum* fed birds and $0.48 \pm 0.14$ for restricted birds. When these estimates were pooled with the heritability estimates from half-sib analyses, the combined estimate for *ad libitum* fed birds was again lower than for restricted birds (Table 4).

The modified Richards curve explained just 62% of the total variation in wing length in control quail and 58% in restricted quail. Obviously, the growth of the wing could not be described by a sigmoid growth model satisfactorily (Figure 7) since the period of measurement did not cover the entire growing period. Because wings continued to grow beyond 44 days of age, data were not fitted to the modified Richards curve.

### 4. Discussion

(i) *Growth patterns and environmental sensitivity*

The four traits, body weight, tarsus length, length of the third primary feather, and wing length had very different growth patterns under *ad libitum* and 30% restricted feeding regimes. The third primary covert feather grew most rapidly. It was not present at hatching and reached its asymptotic value at about 20 days of age. This was reflected by the lowest $T$-parameter of all traits, which was 13.4 days for *ad libitum* fed chicks and about 16 days for restricted chicks. The tarsus had the largest $T$-value of almost 60 days. The growth period of weight was intermediate (about 40 days).

A feature common to all four traits was that sexual dimorphism disappeared under restricted feeding. This suggests that an increased feed intake in females was required for sexual dimorphism in body size.

(ii) *Heritabilities of growth curve parameters and final size*

Heritabilities of body weight and tarsus length often approached unity and were very high at 44 days of age. These high estimates agree with data in the literature on Japanese Quail. The heritability of body weight was reported to be 0.82 (Garwood & Diehl, 1987) and 0.84 for the metatarsus (Isogai, 1971). Data also agree with high responses to selection for body weight in Japanese Quail (Marks, 1988).

For body weight, heritabilities in males tended to be higher than in females, which has been previously reported by Sefton & Siegel, 1974. This was especially
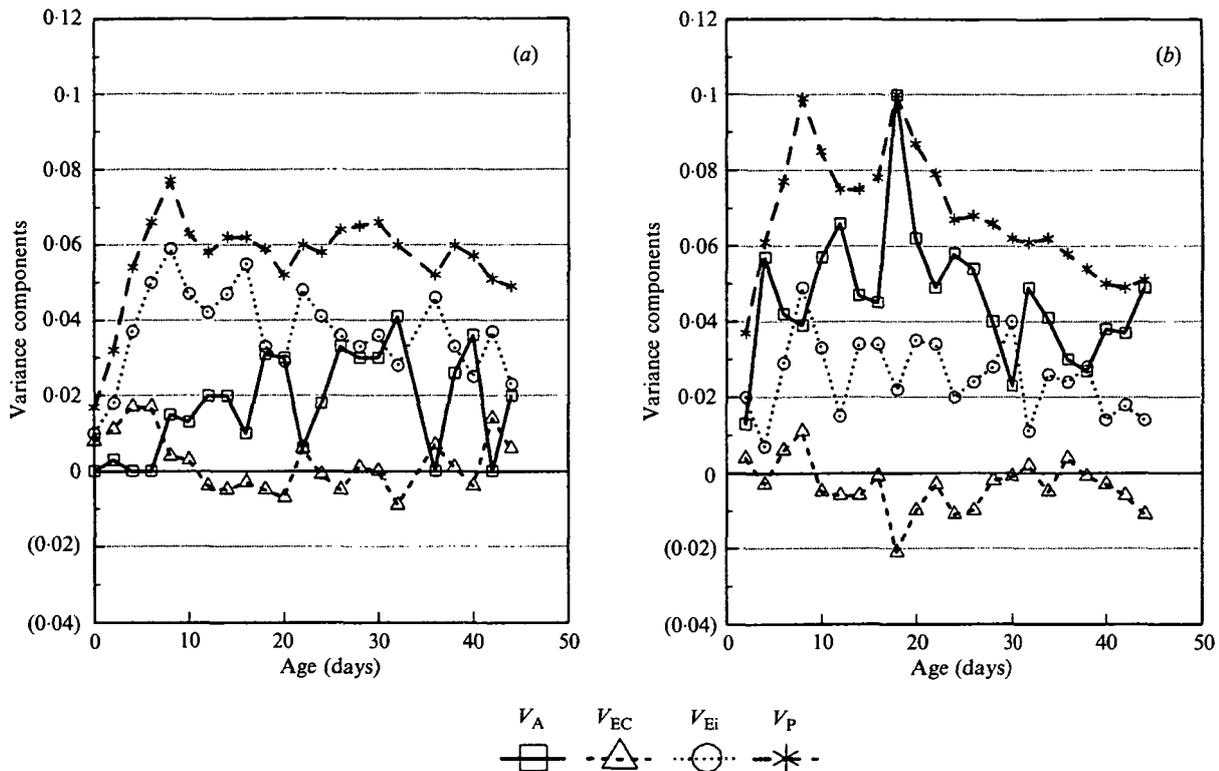
Fig. 8. Variance components based on wing length throughout growth for *ad libitum* fed chicks (*a*) and 30 % restricted chicks. (*b*) For symbols see Fig. 2.

true for females in the *ad libitum* fed treatment that started reproduction during the experiment. Female weight during puberty is complicated by the growth of ovaries and other reproductive tissues (Sefton & Siegel, 1974). In *ad libitum* fed females puberty started as early as day 34. There is no obvious explanation for the zero heritability estimates in *ad libitum* fed and restricted females from hatching to day 4.

Although there was good agreement between heritability estimates derived from half-sib analyses and from parent–offspring regressions, half-sib analyses tended to yield higher estimates. In this context it is important to consider that the experimental design was planned to minimize random environmental variance, and in this it was very successful for body weight and tarsus length. These heritability estimates therefore could not be applied to a natural or even a different laboratory situation. The estimates presented show the potential expression of genetic variation for these traits. The estimation of variance components is, of course, not error-free and can commonly lead to negative 'variance components' (Bridges & Knapp, 1987), or heritabilities larger than one. Standard errors of half-sib analyses as calculated by the 'delta method' (see Methods) appear to be unrealistically low. For that reason, the patterns of genetic and environmental variances were presented graphically, rather than as actual values.

The usefulness of curve-fitting, especially to the complex Richards curve, has been questioned (see

Zach, 1988). In this case, the estimated asymptotes agreed very well with the measured endpoints of growth. The estimate of the growth period of tarsus length lies beyond the period of measurement ($T \approx 60$ days, 44 days were measured). The estimated asymptote however, (29·54 mm for *ad libitum* fed birds) agrees very well with the tarsus length of the parental generation (29·15 ± 8·78 mm) and is larger than the tarsus length measured at 44 days of age (Table 2). The growth period of tarsus length seemed longer than the period of measurement, but the good fit of the model validates its use. At the end of measurement growth rates of tarsus length were probably smaller than the measurement error of this trait.

Table 4 gives an overview of heritabilities under *ad libitum* and restricted feeding and the heritabilities of the growth curve parameters of the four traits. The heritabilities of the estimated asymptotes corresponded well with the heritabilities of the endpoints of growth. The shape-parameter (*m*-parameter) of tarsus growth was moderately heritable in restricted birds (Table 4). In several species (chicken, sheep, and mice) the shape parameter of the growth curve also had low or no heritabilities (Kirkpatrick and Lofsvold, manuscript in preparation). Heritabilities of the growth period (*T*-parameter) varied among traits. Tarsus length had a highly heritable growth period, whereas the heritability of the growth period of body weight was only moderate and the growth period of the primary covert feather was essentially zero.

As in the computer simulation (Gebhardt-Henrich, 1992), the trait with a heritable growth period (tarsus length) had a higher heritability under restricted feeding. This could be visualized as birds that have a short growth period could prolong it under restricted feeding and reach a long tarsus, whereas quail with a 'naturally' long growth period could not compensate by a prolongation of the growth period. The genetic variation of the growth period would then add to the genetic variation of final size generated by genetic variation in the asymptote under these (restricted feeding) conditions. Under *ad libitum* feeding, quail with short or long growth periods would display only genetic variation in the asymptote and the genetic variation of the growth period would not be expressed in the final value.

Heritabilities have notoriously high standard errors, which makes conclusions from this study tentative. Further investigation is needed to verify these results. Nevertheless, heritabilities of different traits were affected differently by feed restriction and this could have been influenced by heritabilities of growth components.

### (iv) *Compensatory growth and conclusions*

Compensatory growth following restricted feeding was evident for all four traits, but to different degrees. It was complete only for wing length: wing length was the same for *ad libitum* fed and restricted quail. Compensatory growth in all traits consisted of continuing increases in gains after the gains of *ad libitum* fed quail decreased and a prolongation of the growth period in feed restricted birds. This may be a general phenomenon. In Ipswich sparrows growth and damping rates (related to the *T*-parameter) were highly correlated (Ross, 1980). Thus, variation in growth rates can result in variation in the time to reach the asymptote apart from the asymptote itself (Ross, 1980).

Compensatory growth, which is often shown by a decrease in variance over time, was slower in restricted birds. Pre-hatching maternal effects lasted longer in restricted quail, and correlations between measurements at advancing ages (not shown) were higher in restricted quail. Therefore, early size was much more decisive (or of a higher predictive value) for later growth under restricted conditions. Individual size differences due to maternal effects or random environmental variation were unimportant for later growth under *ad libitum* access to feed.

### 5. Acknowledgements

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