

## HERITABILITY AND GENETIC AND PHENOTYPIC CORRELATION OF SKULL TRAITS IN THE RABBIT

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**Chi-Ming Huang** (1987) Heritability and genetic and phenotypic correlation of skull traits in the rabbit. *Bull. Inst. Zool., Academia Sinica* 26(2): 133-141. Heritabilities and genetic and phenotypic correlations of twenty six skull measurements in the domestic rabbit were estimated. Heritability estimates for the majority of these traits were moderately high, ranging from 0.4 to 0.6. Genetic and phenotypic correlations were also generally very high. The high correlations between genetic components of the upper and the lower jaw suggested that these traits were controlled, at least in part, by the same genes.

Studies concerning genetic variation for economically important characters in animals have been numerous while those dealing with skeletal traits are rather scanty. In studies concerned with genetic variation in mice, moderately high heritability estimates in dental traits both in house mice (Bader, 1965; Leamy and Touchberry, 1974) and *Peromyscus leucopus* (Leamy and Bader, 1968) have been reported. A moderately high heritability has been reported for seven traits of the skull (Leamy, 1974) and for mandible size (Murai, 1975) in mice. Hereditary variation in various components of the cranio-facial complex have been reported in several twin studies in man. For example, Horowitz and colleagues (1960) showed that there was a highly significant genetic variation in the anterior cranial base, mandibular body height and total and lower facial height. In a similar study Hunter (1965) and Dudas and Sassouni (1973) reported significant genetic components of variability for total, upper and lower facial

height as well as for corpus, total mandible and ramus length. Nakata *et al.* (1974) investigated 33 cranio-facial traits in a twin study by cephalometric measurement and reported a moderately high heritability of 0.4 to 0.6 for most of the traits measured.

It has also been suggested that there is an independent genetic determination of the upper and lower jaw (Nakata *et al.*, 1974), and even within the upper jaw there appeared to be independent genetic influences on maxillary height and depth. In a study in dogs, Stockard (1941) reported that the genes determining length of the maxilla and mandible are inherited independently.

The purpose of the present study is to obtain information regarding the hereditary natures and interrelationships of various skull measurements in the domestic rabbit.

### MATERIALS AND METHODS

Rabbits used in this study were obtained from a colony developed from a crossbred

foundation for a two-way selection experiment involving post-weaning weight gain and gross feed efficiency (Vogt, 1979; Huang *et al.*, 1981). Four breeds were used: Dutch, Siamese Satin, New Zealand White and Flemish Giant. All possible two-breed crosses were made in the first generation and four-breed crosses in the second generation. In each of the subsequent four generations individuals were randomly selected for mating. Four lines were formed in the seventh generation. Two lines were assigned for two-way selection of body weight gain and the other two for gross feed efficiency. Animals were generally available for sacrifice and subsequent inclusion in the present study at about 12 weeks of age. In some cases, animals were sacrificed at 8 weeks of age. Mature animals from the breeding colony were sacrificed at various ages. At sacrifice, each head was skinned, identified and dehydrated in the

drier at 50°C for 5-7 days. Soft tissues were subsequently removed by dermestid beetles.

Twenty six linear measurements were made on each skull with a Helios precision dial caliper (J & S Precision Scientific Measuring Instrument Company, New York) and recorded in millimeters. Reference points on skull measurements were obtained according to Craigie (1960) and Mclaughlin (1970) and are illustrated in Fig. 1. Of these measurements, 13 had two recorded values representing right and left sides of the skull. These twenty-six skull measurements consisted of two major components, a cranial and maxillary component (measurements 1 to 17) as well as a mandibular component (measurements 18 to 26). A detailed description of each of these characters is given below. Asterisks denote both right and left sides of skull measurements being taken. These included skull measurements 2 to 6 and 18 to 25.

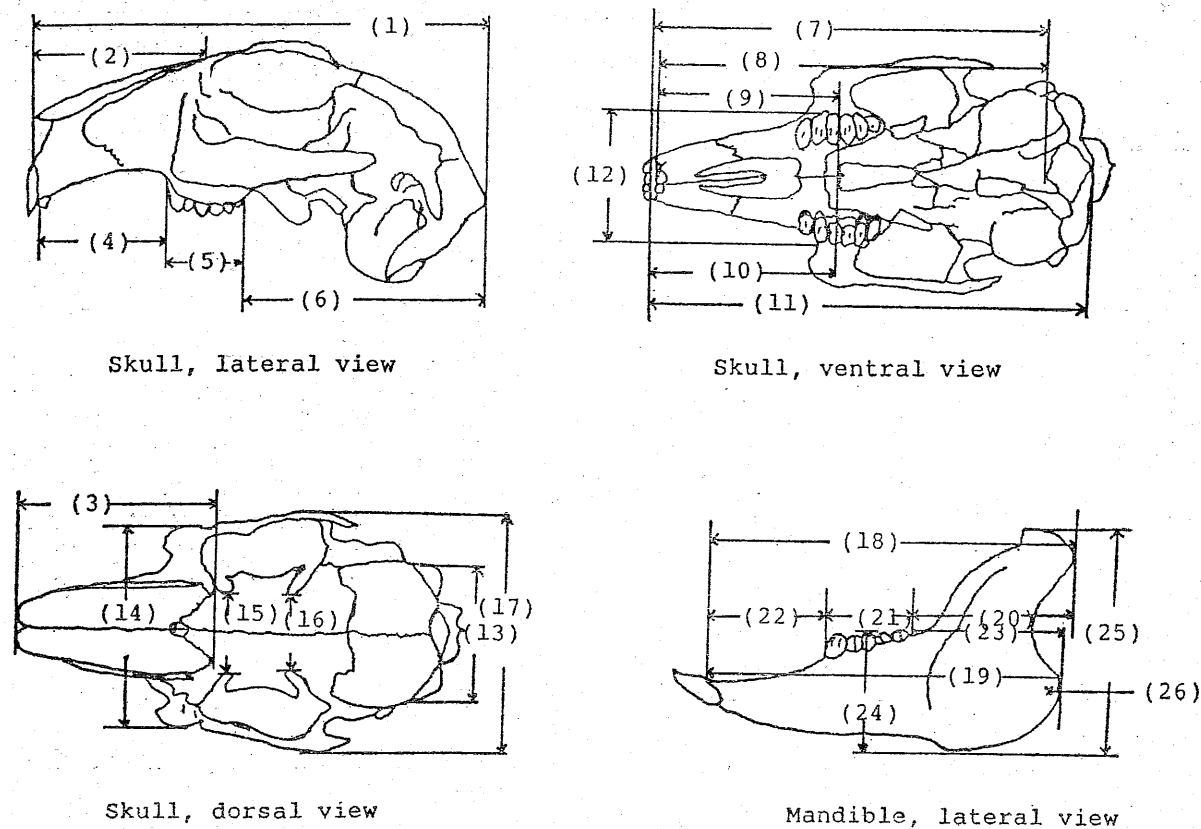


Fig. 1. Landmark for rabbit skull measurement.

- 1) Skull length- the greatest length of skull not including incisors, from external occipital protuberance to anterior tip of premaxilla.
- 2)\* Superior premaxilla length.
- 3)\* Greatest nasal length.
- 4)\* Maxillary diastema- from anteriormost rim of alveolus of first cheek tooth to the anterior rim of the second incisors.
- 5)\* Length of maxillary cheek tooth row.
- 6)\* Length from external occipital protuberance to the alveolar edge of the third molar.
- 7) Basal length- from the anterior edge of the premaxillae to the anteriormost point on the ventral border of the foramen magnum.
- 8) Basilar length- from the posterior margins of the alveoli of the first upper incisors to the anteriormost point on the lower border of the foramen magnum.
- 9) Palatilar length- from the anterior edge of alveolus of second incisors to anteriormost point on posterior edge of palate.
- 10) Palatal length- from anterior edge of premaxillae to anteriormost point on posterior edge of palate.
- 11) Condylbasal length- from the anterior edge of the premaxillae to the posteriormost projection of the occipital condyles.
- 12) Greatest outside width between the second premolars of maxilla.
- 13) Mastoid breadth- greatest outside width between the mastoid processes.
- 14) Greatest outside width between two spina masseterica.
- 15) Least interorbital breadth- least distance between the orbits anterior to the supra-orbital processes.
- 16) Postorbital constriction- least distance across skull posterior to the postorbital process.
- 17) Zygomatic breadth- greatest outside width between two zygomatic bones.
- 18)\* Greatest length of mandible- from posterior edge of condyloid process to dorsal rim of incisor alveolus.
- 19)\* Distance from pterygoid tuberosities to dorsal rim of incisor alveolus.
- 20)\* Length from posterior edge of condyloid process of mandible to posterior border of alveolus of the third molar.
- 21)\* Length of mandibular cheek teeth row.
- 22)\* Mandibular diastema- from anteriormost rim of first cheek tooth alveolus to dorsal rim of incisor.
- 23)\* Length from pterygoid tuberosities to posterior border of alveolus of the third molar.
- 24)\* Greatest height from the top of the first molar to the base of ramus resting upright on a flat surface in perpendicular angle.
- 25)\* Greatest height from the top of condyloid process to the base of ramus resting upright on a flat surface in perpendicular angle.
- 26) The outside width between two masseteric tuberosities.

All skull measurements were adjusted for the effects of sex, occlusion status and age at sacrifice using animals in the eighth generation because of the large sample size ( $N=540$ ) and great age variation in that generation. Two models of the least squares method were employed for adjusting the skull measurements (Harvey, 1960). In the first model, age was treated as a discrete variable. The total age range was divided into several classes to which individuals were assigned based on the age at sacrifice. The second model specified age as a continuous variable, and the age of each animal at sacrifice was fitted with polynomial models up to the seventh order. All interactions between the main effects were assumed to be negligible. As littermates were sacrificed at varying age because of scheduling and selection for breeding, the analysis of variance was performed on a within litter basis. Data were adjusted for all significant effects prior to genetic analysis.

Heritability of skull measurements was estimated by the methods of parent-offspring

regression which included regression of offspring on sire, dam and mid-parent and by fullsib correlation on a within selection-line basis (Falconer, 1981). Only data on animals with normal occlusion were selected for these estimates. The full-sib correlation was computed as intraclass correlation based on the estimation of variance components between and within sibships. All pedigrees were traced back to the third generation for the determination of any inbreeding. Heritability estimates were adjusted for the amount of inbreeding (Lush, 1948). Genetic correlation was derived from the analysis of covariance between two traits from the full-sib correlation ( $r = COV_b / \sqrt{V_b(x)V_b(y)}$ ).  $COV_b$  was the between sibship covariance of two traits,  $X$  and  $Y$ .  $V_b(x)$  was the between sibship variance component of trait  $X$  and  $V_b(y)$  the corresponding variance component of trait  $Y$ . Phenotypic correlation between

sibs was estimated as  $r = COV_w + COV_b / \sqrt{[V_w(x) + V_b(x)][V_w(y) + V_b(y)]}$ , where  $COV_w$  and  $COV_b$  were, respectively, within and between sibship covariance.  $V_w(x)$  and  $V_w(y)$  were the within and between sibship variance component of two traits,  $X$  and  $Y$ , and  $V_b(x)$  and  $V_b(y)$  were the corresponding within and between sibship variance component of two traits.

## RESULTS

Individual rabbit skulls representing all animals from three generations, seventh, eighth, and ninth, were measured. All animals in the seventh generation were adult animals aged five months or older. The number of male and female animals were 61 and 67 respectively. The eighth generation provided 540 skulls, approximately equally represented with respect to sex and occlusion status.

TABLE 1  
Mean and standard deviation of skull measurements  
(millimeters) of sire and dam

Measure- ment <sup>1)</sup>	Sire (n=54)		Dam (n=64)		Measure- ment	Sire (n=54)		Dam (n=64)	
	Mean	SD	Mean	SD		Mean	SD	Mean	SD
1	90.89	3.99	90.90	3.41	16	12.49	0.75	12.51	0.81
2L	52.30	2.67	52.65	2.53	17	46.31	1.74	45.09	2.01
2R	52.33	2.66	52.59	2.48	18L	71.23	3.15	71.24	2.83
3L	45.21	3.11	45.55	2.84	18R	71.41	3.34	71.02	2.93
3R	45.34	3.26	45.77	2.84	19L	65.76	2.98	66.02	2.65
4L	28.32	2.27	28.46	1.60	19R	65.82	3.06	65.72	2.70
4R	28.26	2.22	28.24	1.60	20L	34.36	1.94	34.16	1.60
5L	16.00	0.67	15.93	0.68	20R	34.44	2.01	34.11	1.76
5R	16.01	0.70	15.93	0.67	21L	15.77	0.84	15.58	0.85
6L	48.31	2.11	48.00	1.67	21R	15.81	0.77	15.60	0.85
6R	48.14	2.07	47.91	1.73	22L	21.99	1.47	22.21	1.26
7	74.58	3.74	74.66	3.35	22R	22.03	1.50	22.13	1.29
8	72.37	3.76	72.41	3.30	23L	29.13	1.65	29.10	1.42
9	37.59	2.26	37.74	2.02	23R	29.05	1.72	28.90	1.54
10	39.61	2.35	39.78	2.08	24L	21.35	1.11	21.09	1.18
11	82.89	4.12	81.91	3.61	24R	21.40	1.11	21.13	1.17
12	23.45	0.89	23.62	1.00	25L	45.70	2.52	45.23	2.29
13	33.26	1.23	33.30	1.38	25R	45.90	2.53	45.33	2.40
14	45.01	1.41	44.61	1.88	26	46.32	2.35	44.30	2.55
15	15.31	1.29	15.32	1.34					

<sup>1)</sup>L=Left side measurement; R=Right side measurement

TABLE 2  
Heritability estimates of skull measurements from parent offspring regression  
and full-sib correlation

Measure- ment <sup>1)</sup>	Sire- offspring	Dam- offspring	Mid-parent offspring	Full-sib correlation
1	0.43±0.11	0.52±0.13	0.45±0.10	0.51
2L	0.64±0.10	0.62±0.13	0.69±0.10	0.45
2R	0.64±0.11	0.67±0.13	0.78±0.10	0.45
3L	0.45±0.11	0.35±0.14	0.54±0.13	0.51
3R	0.41±0.10	0.25±0.14NS	0.41±0.13	0.47
4L	0.38±0.10	0.39±0.12	0.36±0.10	0.45
4R	0.34±0.09	0.40±0.12	0.37±0.10	0.46
5L	0.33±0.11	0.42±0.12	0.45±0.09	0.41
5R	0.34±0.10	0.39±0.12	0.40±0.08	0.43
6L	0.62±0.11	0.72±0.14	0.56±0.11	0.50
6R	0.63±0.11	0.70±0.13	0.56±0.10	0.50
7	0.42±0.11	0.45±0.13	0.48±0.11	0.48
8	0.41±0.10	0.49±0.13	0.45±0.10	0.48
9	0.41±0.11	0.49±0.13	0.43±0.10	0.43
10	0.39±0.09	0.49±0.13	0.47±0.10	0.54
11	0.43±0.10	0.43±0.13	0.46±0.11	0.48
12	0.87±0.13	0.78±0.13	0.74±0.11	0.48
13	0.48±0.13	0.67±0.13	0.48±0.12	0.57
14	0.70±0.14	0.69±0.15	0.63±0.13	0.49
15	0.60±0.09	0.50±0.12	0.57±0.11	0.40
16	0.61±0.13	0.71±0.13	0.81±0.09	0.36
17	0.48±0.11	0.57±0.14	0.45±0.12	0.38
18L	0.37±0.10	0.29±0.13*	0.21±0.13NS	0.51
18R	0.42±0.10	0.34±0.13	0.21±0.12NS	0.52
19L	0.40±0.10	0.42±0.12	0.37±0.12	0.52
19R	0.44±0.10	0.42±0.12	0.39±0.11	0.52
20L	0.46±0.10	0.56±0.13	0.36±0.11	0.53
20R	0.58±0.10	0.63±0.13	0.40±0.11	0.53
21L	0.20±0.07	0.23±0.10*	0.25±0.07	0.31
21R	0.12±0.09NS	0.19±0.09*	0.21±0.08	0.26
22L	0.37±0.09	0.23±0.11*	0.25±0.11*	0.49
22R	0.38±0.09	0.22±0.10*	0.28±0.10	0.46
23L	0.42±0.10	0.65±0.13	0.47±0.11	0.49
23R	0.54±0.10	0.67±0.12	0.53±0.10	0.51
24L	0.19±0.09*	0.15±0.12NS	0.22±0.11*	0.30
24R	0.26±0.11*	0.15±0.13NS	0.17±0.12NS	0.34
25L	0.50±0.10	0.42±0.14	0.42±0.13	0.38
25R	0.52±0.10	0.41±0.14	0.39±0.13	0.40
26	0.24±0.15NS	0.75±0.14	0.60±0.14	0.31

<sup>1)</sup>NS=nonsignificant; \*  $p < 0.05$

All other measurements are significant at the 1% level  
L=Left side measurement; R=Right side measurement

TABLE 3  
Phenotypic and genetic correlations of rabbit skull measurements<sup>1)</sup>

	1	2L	3L	4L	5L	6L	7	8	9	10	11	12	13	14	15	16	17	18L	19L	20L	21L	22L	23L	24L	25L	26	
1																											
2L	.86																										
3L	.84	.87																									
4L	.85	.96	.85																								
5L	.97	.96	.95	.88																							
6L	.99	.94	.92	.94	.89																						
7	.99	.96	.94	.97	.92	.98																					
8	.99	.96	.94	.97	.92	.98	1.00																				
9	.97	.96	.94	.97	.90	.95	.97	.97																			
10	.98	.96	.95	.97	.92	.95	.97	.97	.98																		
11	.99	.96	.94	.97	.92	.98	1.00	.99	.97	.97																	
12	.87	.86	.82	.84	.82	.86	.86	.86	.84	.84	.87																
13	.88	.87	.86	.86	.81	.88	.87	.87	.87	.87	.79																
14	.92	.90	.86	.88	.85	.93	.91	.91	.90	.89	.91	.87	.87														
15	.73	.74	.77	.73	.69	.72	.72	.72	.74	.73	.72	.65	.66	.68													
16	---	---	---	---	---	---	---	---	---	---	---	---	---	---	.24												
17	.86	.83	.79	.80	.82	.88	.86	.86	.84	.83	.85	.79	.84	.93	.62	---											
18L	.98	.97	.95	.96	.92	.97	.97	.98	.97	.97	.97	.86	.88	.93	.73	---	.88										
19L	.98	.97	.94	.96	.92	.97	.98	.98	.96	.97	.98	.86	.88	.92	.72	---	.88	.99									
20L	.96	.95	.92	.93	.89	.96	.95	.96	.94	.94	.95	.84	.87	.92	.71	---	.89	.98	.97								
21L	.88	.87	.84	.86	.90	.86	.88	.88	.87	.87	.88	.75	.77	.80	.66	---	.78	.89	.88	.82							
22L	.95	.94	.93	.95	.88	.92	.94	.94	.94	.95	.94	.83	.85	.89	.71	---	.84	.97	.96	.93	.83						
23L	.95	.93	.91	.92	.87	.95	.95	.95	.92	.93	.95	.84	.87	.91	.68	---	.87	.96	.98	.97	.79	.92					
24L	.89	.68	.87	.87	.85	.87	.87	.87	.88	.88	.87	.76	.82	.87	.68	---	.85	.92	.90	.90	.82	.89	.88				
25L	.94	.93	.90	.90	.88	.94	.94	.94	.92	.92	.93	.84	.88	.92	.68	---	.90	.95	.95	.96	.84	.91	.93	.90			
26	.86	.84	.80	.81	.84	.87	.85	.86	.84	.84	.85	.80	.83	.91	.61	---	.93	.88	.88	.88	.79	.84	.87	.85	.89		

<sup>1)</sup> Genetic correlations in the upper triangle and phenotypic correlations in the lower triangle.

For the ninth generation all skulls were obtained from young animals. There were slightly more male than female animals, 207 and 176, respectively. The results of preliminary statistical analysis using polynomial models provided a better fit for adjusting skull measurements.

The means and standard deviations of all adjusted skull measurements for sires and dams of the eighth generation are given in Table 1. In most cases the means for sire's and dam's measurements were quite similar, and remained similar for the ninth generation as well.

Heritability estimates of all skull measurements based on parent-offspring regression and full-sib correlation are shown in Table 2. The estimates were moderately high for most skull measurements. Heritability estimates for sire-offspring regression ranged from 0.12 to 0.87, for dam-offspring regression from 0.15 to 0.78, and for mid-parent offspring regression from 0.17 to 0.81. The coefficients of full-sib correlation ranged from 0.26 to 0.57, estimating one half the heritability plus common environmental effects. Heritability estimates were generally found to be higher for cranial and maxillary components (measurements 1 to 17) than for mandibular components (measurements 18 to 26). Most of the heritability estimates from dam-offspring regressions were generally higher than those estimated from sire-offspring and mid-parent-offspring regressions. This might be attributable to maternal influences. The heritability estimates were highly significant for all but a few measurements, mostly on the mandibular components. Regressions of the mean of all offspring of a given litter on sire, dam, and midparent also gave identical results. Heritability estimates of these same skull traits for animals of the ninth generation were also moderately high and similar to those obtained from the preceding generation.

The results of the analysis of the eighth generation data for genetic and phenotypic correlations are given in Table 3. Only left-

side measurements are shown in the table since both left and right sides give a correlation of nearly 1.0 in all measurements. The genetic correlations were generally highly significant for most skull characters measured with the exception of those measurements 5, 16 and 21. The maxillary cheek teeth row (measurement 5) and the mandibular cheek teeth row (measurement 21) had relatively low genetic correlations with nearly all other skull measurements. Postorbital constriction (measurement 16) was the only trait that had negative genetic correlations with most other skull measurements except for measurements 12, 13, 14, 15 and 17 with which very low genetic correlations existed between these traits. Phenotypic correlations were higher than those of corresponding genetic correlations of two skull measurements. There were no significant phenotypic correlations between postorbital constriction (measurement 16) and any other traits except measurement 15 which was least interorbital breadth.

## DISCUSSION

The level of heritability exhibited by 26 skull measurements in the rabbit, mostly ranging from 0.4 to 0.6, is moderately high. The high heritability estimates obtained for these skeletal characters indicated that adequate amounts of additive genetic variance were present in these characters. The estimates are quite similar and consistent in two generations. This is in agreement with the findings of the few heritability studies on skull and dental traits in mice (Bader, 1965; Leamy and Bader, 1968; Leamy, 1974; Leamy and Touchberry, 1974; Murai, 1975), and cranial-facial traits in man (Nakata *et al.*, 1974). Estimates of heritability by dam-offspring regressions were generally higher than those estimated by sire-offspring and mid-parent offspring regressions. This was presumably due to maternal effects. In all measurements heritability estimates derived from full-sib correlation were higher than

those estimated from parent offspring regression. It is well known for most quantitative traits that full-sib correlations are generally considered as the least reliable method of estimating heritability owing to the presence of components due to common environment plus a fraction of nonadditive variance.

The majority of the animals used in this study were obtained from the selection experiment for weight gain and feed efficiency. Only those animals used in the selection experiment were included in heritability estimates. Analysis of variance showed that there were significant differences in the skull measurements among the four selection lines. Therefore, heritability estimates were analyzed on a within selection line basis. In general, heritability estimated by parent offspring regressions resulted in more significant values among the two low lines than the two high lines indicating a larger amount of genetic variation existed in the low lines.

The generally consistent and high genetic correlations indicate that these skeletal traits are influenced, at least in part, by many of the same genes. It has been reported that mandibular prognathism in the rabbit is due to a simple autosomal recessive inheritance with incomplete penetrance (Huang *et al.*, 1981). This suggests that high genetic correlation is not likely to be caused by linkage. However, genetic correlations estimated from full-sib correlation also include some amount of dominance and epistatic effects. This made the genetic correlation somewhat upwardly inflated. Many of these skull traits were perhaps pleiotropically related to each other, and are being affected by a small number of genes each with large effect. This suggested that many of these cranial, maxillary, and mandibular components were controlled by the same genes. The high genetic correlations within cranial and maxillary components, and within mandibular components, as well as between maxillary and mandibular components suggest that cranial and maxillary components on the upper jaw and mandibular

components on the lower jaw are not inherited independently as reported by several authors (Hughes and Moore, 1941; Stockard, 1941; Nakata *et al.*, 1974; Potter *et al.*, 1976). The low genetic correlations between the maxillary and mandibular cheek teeth row with other skull traits might indicate that these two traits were probably more stable, and the expected response to selection might be small. The negative genetic correlations found between postorbital constriction (measurement 16) and most other skull traits indicated that they would respond to selection in opposite direction. It is not known why this particular skull trait has a negative genetic correlation with others.

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## 兔子頭殼性狀的遺傳力及遺傳與表現型的相關性研究

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兔子的頭殼總共量度二十六種性狀，以評估其遺傳力及遺傳與表現型的相關性，大多數頭殼性狀遺傳力很高，介於 0.4 至 0.6 之間，這些性狀的遺傳及表現型的相關性亦極高，對於頭殼的上顎及下顎的性狀有很高的遺傳相關，顯示這些性狀至少有一部份被相同的遺傳基因所控制。

