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Effect of disruptive selection for body conformation on age variations of femoral morphometric traits, in mice

Summary

The effect of disruptive selection for body conformation on body weight and length, tail length, and femur weight and length at different stages of development (21, 42, 63, and 120 days of age) was analysed in four mouse lines of the CBi stock selected for (CBi+, CBi-) and against (CBi/L, CBi/C) the phenotypic correlation between body weight and tail length, and the unselected control line CBi. As expected, body weight and tail length distributed according to the selection criteria; trunk length (whole body length minus tail length) behaved as body weight at all ages. CBi/L had the highest femoral length ($p<0.01$), and CBi/C attained the highest femoral weight ($p<0.01$). CBi+ and CBi-, harmonically large or small, differed between them and from the control line in both variables ($p<0.001$). These findings further corroborate the proposal that bone mass is markedly affected by the skeleton function as support of soft tissues. The allometric analysis of the regression of femur weight on femur length suggests that, in this model, a) the demand posed by the selective pressure forced each genotype to find a unique solution, b) this response is sex-dependent, and c) genetic determination of the parameters involved in this allometric relationship is, at least, partially independent.

Key words: disruptive selection, body conformation, femur weight, femur length, mice

Zusammenfassung

Titel der Arbeit: **Der Einfluß der disruptiven Selektion nach Körperkonformation auf die Altersvariation der morphometrischen Merkmale des Femurs bei der Maus**

Der Einfluß einer disruptiven Selektion nach Körperkonformation auf die Körpermasse und -länge, Schwanzlänge und Masse bzw. Länge des Femurs im Alter von 21, 42, 63 und 120 Tagen wurde in vier Populationen des CBi-Stammes analysiert. Neben der unselektierten Kontrollpopulation erfolgte die Selektion in den Linien (CBi+, CBi-) auf die phänotypische Korrelation zwischen Körpermasse und Schwanzlänge und in den Linien (CBi/L; CBi/C) gegen diese Korrelation. Wie erwartet, veränderten sich die Körpermasse und Schwanzlänge entsprechend der Selektionskriterien. CBi/L hatte die höchste Femurlänge ($P<0,01$) und CBi/C das höchste Gewicht des Femurs. Die allometrische Analyse der Regression des Femurgewichtes zur -länge zeigte in diesem Modell: a) der Selektionsdruck führte in jeder Linie zu einer anderen Lösung, b) diese Veränderungen sind geschlechtsabhängig und c) die genetische Determination der Regressionsparameter ist teilsweise voneinander unabhängig.

Schlüsselwörter: Disruptive Selektion, Körperkonformation, Femurgewicht, Femurlänge, Maus

Introduction

An efficient production of lean has been, and in some cases still is, a key objective in animal production. This compositional aspect of growth is deeply connected with two other approaches of growth studies: the so-called dimensional and developmental viewpoints.

REEDS et al. (1993) propose the genetic program of the skeleton as the major determinant of postnatal dimensional growth. In this sense, the long bones have a genetically determined proclivity to attain a given length, and once this linear growth ceases it is not reinitiated. In addition, the length of the skeletal components determines the length of the skeletal muscles. Therefore, bones and muscles show an intimate developmental association, accounting for at least 60% of the target fat-free body mass.

Adult mice from four lines (CBi+, CBi-, CBi/C and CBi/L), artificially selected for body conformation using skeletal length as part of the selective criterion, have shown extreme modifications in morphometric skeletal traits and femoral histomorphometry (DI MASSO et al., 1991a; 1998), and in bone biomechanics (DI MASSO et al., 1997b). As body weight was the other trait used for selecting these lines, and as the skeletal mass alters in response to the functional demand (FROST, 1987), the objective of this study was to evaluate age-related changes of body morphometric traits in these mouse lines, particularly those concerning femur length and femur weight relationships.

Materials and Methods

Mice of the CBi stock, sampled from generation 58, were used. The animals belonged to four inbred strains obtained by divergent selection for body conformation (CBi+, CBi-, CBi/C and CBi/L), and to the unselected control line CBi (DI MASSO et al., 1991b). Briefly, the four lines were the result of two selection experiments that used as the selective criterion a quantitative index combining body weight and tail length at 49 days of age, two variables positively correlated ($r_P = 0.56$, $r_G = 0.60$) in the base population. Two lines were derived favouring this positive association (agonistic selection: CBi+, high body weight-long tail; CBi-, low body weight-short tail) while the other two were produced by selection against the phenotypic correlation (antagonistic selection: CBi/C, high body weight-short tail; CBi/L, low body weight-long tail). Throughout the selection experiments the theoretical effective number for each line was Ne=12.8 (FALCONER, 1989); 4 males and 16 females per generation were selected as breeders, without overlapping generations. The selection index changed from null values in the base population to (mean ± SEM, in males and females, respectively), CBi/C: 4.19±0.10, 5.39±0.17; CBi/L: -2.38±0.09, -2.37±0.10; CBi+: 6.85±0.29, 7.79±0.32; CBi-: -6.71±0.17, -4.95±0.19, in generation 58. Because of limited population size, the mean inbreeding coefficient in generation 58 varied from 0.92 for CBi animals to 0.97 for CBi+.

Mice were kept in a standard fashion in a room at 22±2 °C, and water and food (Cargill Laboratory Chow, pelletized) were provided *ad libitum*. Twelve males and 12 females chosen at random from the contemporary populations of each genotype were used. The animals were sacrificed by ether overexposure at 21, 42, 63, and 120 days of age. Immediately afterwards, each mouse was weighed to the nearest 0.1 g and its total body and tail length measured to the nearest mm. Trunk length was estimated by subtracting tail length from total body length.

The right femur was excised, manually dissected to remove muscle and dried at 100-105°C until constant weight. The bone was weighed and its length, the distance from the greatest trochanter to the medial condyle (LEAMY, 1974), measured with a sliding vernier caliper.

Data were analysed using a three-way analysis of variance (SOKAL and ROHLF, 1969) to estimate the effect of genotype, sex and age on each variable measured. The changes of the relationship between femur length and femur dry weight with age were computed using the equation $\log y = \log a + x \log b$, since the arithmetic plot of femur weight against femur length had an exponential trend; x and y are femur length and weight respectively, $\log a$ being the y-intercept, which estimates the initial values and $\log b$, the slope, the relative rate of change of the relationship with age. This equation is the logarithmic form of the exponential growth curve $y = ab^x$ (HUXLEY, 1932). Differences among regression coefficients and adjusted means between genotypes within sex, or between sexes within genotype, were analysed by an analysis of covariance (SNEDECOR and COCHRAN, 1967).

Results

Tables 1, 2 and 3 show body weight, tail length and trunk length for males and females of the five genotypes, at the four ages studied. These variables accurately describe body conformation of each line: body weight and tail length were actually used in the selection, while trunk length was closely associated with body weight.

Table 1
Age-related changes in body weight (mean ± standard error) of male and female mice selected for body conformation (Altersabhängige Veränderungen der Körpermasse (Mittelwert und Standardfehler) von männlichen und weiblichen Mäusen nach Selektion auf Körperkonformation)

Age (days)		Genotypes				
		CBi+	CBi-	CBi	CBi/L	CBi/C
	Males					
21		11.3±0.52	8.7±0.30	9.2±0.64	9.2±0.54	13.7±0.82
42		38.4±0.72	23.4±0.32	28.9±0.58	25.1±1.24	36.0±1.66
63		45.1±0.51	26.2±0.31	33.8±0.29	31.5±0.83	42.4±1.06
120		50.4±1.33	29.7±0.47	38.7±0.97	36.5±0.62	47.6±1.04
	Females					
21		12.0±0.74	7.9±0.21	9.3±0.59	10.2±0.50	12.3±0.86
42		33.5±0.73	19.0±0.42	23.0±0.30	21.9±0.71	30.3±0.81
63		39.3±1.10	22.6±0.34	27.0±0.47	26.3±0.71	39.7±0.66
120		48.3±0.97	25.5±0.51	32.3±1.01	31.7±0.43	43.6±1.08

*Unit of measure, g
Number of animals per genotype-sex-age group: 12
See text (Results) for significance of the difference between groups (Table 1-5)

The analysis of body weight showed significant effects of genotype, sex, and age and the first-order interactions (genotype x age) and (sex x age) ($p<0.001$). The second-order interaction (genotype x sex x age) was not significant ($p>0.05$), indicating that (genotype x sex) groups did not differ in their body weight-age patterns. As expected, the lines distributed according to the criterion of selection: CBi+ and CBi/C mice,

Table 2
Age-related changes in tail length (mean ± standard error) of male and female mice selected for body conformation (Alterabhängige Veränderungen der Schwanzlänge (Mittelwert und Standardfehler) von männlichen und weiblichen Mäusen nach Selektion auf Körperkonformation)

Age (days)		Genotypes				
		CBi+	CBi-	CBi	CBi/L	CBi/C
	Males					
21		60.8±2.04	45.3±0.35	52.3±1.71	69.6±1.19	52.1±1.86
42		105.1±1.04	71.7±0.99	86.4±1.22	104.5±2.93	79.8±1.79
63		110.0±1.03	75.8±1.17	91.5±1.28	115.1±1.80	81.9±1.16
120		111.8±0.82	79.9±0.67	92.9±1.05	122.1±0.50	86.7±0.96
	Females					
21		62.1±1.83	45.4±1.19	53.7±1.48	72.0±1.48	50.8±2.32
42		103.8±1.37	70.4±1.64	85.3±0.92	102.9±1.64	76.3±1.90
63		110.1±1.07	75.6±0.66	89.5±0.87	109.6±0.87	85.3±0.54
120		114.3±0.85	80.2±1.19	92.0±0.66	120.6±0.96	87.6±1.16

*Unit of measure, mm
Number of animals per genotype-sex-age group: 12

Table 3
Age-related changes in trunk length (mean ± standard error) of male and female mice selected for body conformation (Altersabhängige Veränderungen der Rumpflänge (Mittelwert und Standardfehler) von männlichen und weiblichen Mäusen nach Selektion auf Körperkonformation)

Age (days)		Genotypes				
		CBi+	CBi-	CBi	CBi/L	CBi/C
	Males					
21		67.0±1.11	62.5±0.77	64.2±1.24	65.2±0.81	74.1±1.58
42		102.7±0.73	88.0±0.65	93.3±0.57	92.4±1.00	100.5±1.05
63		107.9±0.75	89.8±0.46	98.1±0.43	98.5±0.96	106.3±0.47
120		111.8±1.12	94.2±1.05	101.8±0.78	104.3±0.81	110.0±0.76
	Females					
21		68.6±1.29	60.8±0.73	63.9±1.03	66.3±1.32	70.8±1.47
42		98.8±0.95	81.4±0.50	88.8±0.47	88.8±0.96	95.4±1.04
63		105.6±0.79	86.8±0.52	93.5±0.72	94.2±0.61	103.3±0.82
120		112.2±0.97	91.5±0.68	100.2±0.65	102.7±0.62	107.4±0.86

Unit of measure, mm
Number of animals per genotype-sex-age group: 12

selected for high body weight, were heavier than CBi, whereas their counterparts (CBi- and CBi/L), selected for low body weight, were lighter than controls. CBi/L females were an exception, since they did not differ significantly from CBi females. Sexual dimorphism was apparent after 42 days of age, males being larger than females.

Tail length exhibited significant effects of genotype and age ($p<0.001$). The only significant interaction, (genotype x age) ($p<0.001$), denotes differences among lines, but not between sexes, in tail growth patterns. Tail length agreed with the selection criterion utilized. When compared with the control line, CBi- and CBi/C mice, negatively selected for tail length, had shorter tails whereas CBi+ and CBi/L mice, showed longer tails. These differences were evident in both sexes and, overall, could be observed at all ages analysed.

The lines differed significantly in trunk length, a variable not directly selected but closely related to the selection index. Significant effects of genotype, sex and age were observed ($p<0.001$). The three first-order interactions (genotype x age), (genotype x sex) and (sex x age) were also significant ($p<0.01$). CBi+ and CBi- differed between them and with the control line CBi at all ages. These selected lines resulted, respectively, harmonically large and small. Trunk length of CBi/C and CBi/L mice, generated by antagonistic selection, was determined by the response in body weight. CBi/C had a longer trunk than CBi/L and CBi at all ages. On the contrary, CBi/L had a trunk length similar to that of CBi, but at 120 days when it was significantly longer.
Tables 4 and 5 show absolute femoral length and weight at different ages. The statistical analysis of femoral length revealed significant effects of genotype and age ($p<0.001$), as well as significant interactions (genotype x sex), (genotype x age), and

Table 4
Age-related changes in femoral length (mean ± standard error) of male and female mice selected for body conformation (Altersabhängige Veränderungen der Femurlänge (Mittelwert und Standardfehler) von männlichen und weiblichen Mäusen nach Selektion auf Körperkonformation)

Age (days)		Genotypes				
		CBi+	CBi-	CBi	CBi/L	CBi/C
	Males					
21		10.2±0.14	9.6±0.13	9.4±0.20	10.2±0.13	10.7±0.11
42		14.3±0.13	13.2±0.06	13.7±0.13	14.4±0.17	14.5±0.22
63		15.6±.0.09	14.3±0.10	14.7±0.07	16.0±0.09	15.9±0.10
120		15.7±0.13	14.4±0.08	15.2±0.10	17.0±0.08	16.1±0.07
	Females					
21		10.0±0.18	9.3±0.08	9.4±0.16	10.4±0.13	10.3±0.18
42		14.4±0.21	12.9±0.16	13.3±0.07	14.4±0.14	14.1±0.12
63		15.9±0.10	14.2±0.08	14.4±0.14	15.9±0.11	16.1±0.17
120		16.8±0.13	15.0±0.11	15.7±.0.06	17.4±0.07	16.6±0.08

Unit of measure, mm
Number of animals per genotype-sex-age group: 12

Table 5
Age-related changes in femoral dry weight (mean ± standard error) of male and female mice selected for body conformation (Altersabhängige Veränderungen des Trockengewichts des Femurs (Mittelwert und Standardfehler) von männlichen und weiblichen Mäusen nach Selektion auf Körperkonformation)

Age (days)		Genotypes				
		CBi+	CBi-	CBi	CBi/L	CBi/C
	Males					
21		16.6±0.85	12.8±0.66	12.7±0.64	13.0±0.32	17.6±0.65
42		53.6±1.06	33.7±0.66	38.9±1.08	41.0±1.72	54.3±1.99
63		68.3±1.19	41.7±0.67	51.2±0.81	55.5±1.38	68.9±1.59
120		74.1±0.72	45.9±0.64	55.6±0.85	65.0±1.14	76.6±1.27
	Females					
21		16.0±0.85	10.8±0.26	13.3±0.55	14.9±0.84	16.8±1.12
42		50.0±1.55	28.5±1.06	34.5±0.71	36.2±1.38	47.9±1.80
63		68.0±1.37	39.0±0.64	42.8±0.74	50.1±1.80	69.2±1.62
120		77.5±1.39	46.5±0.75	53.3±1.58	65.7±0.97	80.3±1.18

Unit of measure, mg
Number of animals per genotype-sex-age group: 12

(sex x age) ($p<0.01$). Comparisons between genotypes - within sex showed that mice positively selected for body weight (CBi+ and CBi/C) increased their femoral length in a similar amount, though they were selected for long and short tail length, respectively. Femur length in mice negatively selected for body weight responded to the selective pressure for tail length as expected: CBi- mice (low body weight, short tail) decreased femoral length when compared with CBi, while CBi/L animals (low body weight, long tail) increased it. It should be remarked that 120 days old CBi/L mice attained the longest femurs.

Femoral dry weight presented significant differences ($p<0.001$) due to genotype and age, and, at variance with length, it demonstrated a sex effect ($p<0.001$). Both the three first-order interactions and the second-order interaction (genotype x sex x age) were also significant ($p<0.025$), suggesting that each group (genotype x sex) increases the femoral mass at a different rate. CBi+ and CBi-, the lines obtained by agonistic selection, differed significantly between them and with the control CBi. CBi+ femurs were heavier while CBi-'s were lighter than those of CBi. The mice of the antagonistic experiment, CBi/C and CBi/L also differed significantly between them and with CBi ($p<0.01$), but their femurs were both heavier than CBi's.

Table 6 illustrates the nature of the relationship between femoral length and weight in the age interval analysed, for each genotype and sex. The high values of the determination coefficient (R^2) indicate that the logarithmic form of the exponential equation is a good estimate of the relationship between femur length and femur dry weight. Perusal of the table shows that the genotypes differ both in the initial values

Table 6

Regression parameters (y-intercept and slope) for the relationship between femur length and femur dry weight of male and female mice selected for body conformation (Regressionsparameter (a, b) zwischen den Merkmalen Femurlänge und -gewicht von männlichen und weiblichen Mäusen nach Selektion auf Körperkonformation)

Selection	Genotype	Parameters					
		Males			Females		
		a	b	r^2	a	b	r^2
Agonistic	CBi+	* ***	0.266 § (0.008)	0.96	***	0.238 (0.006) *	0.98
	CBi-		0.255 (0.010)	0.94		0.253 (0.006)	0.96
Unselected control	CBi	*	0.256 (0.006) *	0.97		0.227 *** (0.006) *	0.97
Antagonistic	CBi/L		0.236 (0.007)	0.97	***	0.217 (0.005)	0.97
	CBi/C	*	0.265 ** (0.007)	0.97		0.248 *** (0.007)	0.97

§ mean (standard error); Significance of the difference between genotypes: *** $p<0.001$; ** $p<0.01$; * $p<0.05$

(*a*) of these variables and in the manner the relationship changes with aging (*b*). The agonistically selected males had similar slopes and differed significantly in the elevation of the regression lines (CBi+>CBi>CBi-). CBi- female mice showed the highest slope value while CBi+ females had similar slope but higher adjusted mean than CBi. In the antagonistic selected lines, CBi/L males showed the lowest slope value while CBi and CBi/C, having a similar estimate of *b*, differed in the elevation of their regression lines (CBi/C > CBi). A different response was evident in females. CBi/C mice had the highest slope whereas CBi/L and CBi did not differ in their slopes but showed different elevations (CBi>CBi/L). Sexual dimorphism in the slope was apparent in all genotypes except CBi-.

Discussion

Throughout life, the mass of many organs alters in response to changes in the physical or metabolic work that each is called upon to perform (REEDS and FIOROTTO, 1990). The skeleton, being the scaffold that bears the weight of soft tissues, must adapt structurally to respond to the mechanic demand posed by the biomass it has to support. Because skeleton traits show genetic variation, it should be expected that the structural support system undergoes modifications resulting from selection for body weight as it has been described by TRUSLOVE (1976). The criterion used to obtain the lines herein described was tailored to maximize differences in body weight and skeleton length, favouring (agonistic selection) or opposing (antagonistic selection) to the phenotypic correlation between these variables. Results indicate that on selecting both characters, the changes observed were limited primarily by the response to selection for body weight. Genotypes CBi+ and CBi/C had longer trunks than CBi because they were both selected for high body weight, though CBi/C animals were also selected for short tail. CBi- mice showed the shortest body length as a response to the negative selection in body weight and length. Genotype CBi/L, on the other hand, did not modify its trunk length, thus suggesting that there is a weight-dependent genetic mechanism involved in the response to selection for skeleton length.

The response in femoral length was different in each selection experiment. Agonistic selection showed the expected response, when compared with the control line: a longer bone in the positively selected line and a shorter one in the negatively selected branch. This finding indicates that selection of harmonically large or small mice causes a modification in the size of the femur that is the consequence of the selective pressure on both body weight and skeleton length, thus maintaining its structural fitness to support the biomass. On the other hand, the antagonistic selection, showed that the response in size of a bone like the femur is related to its support function, and, as such, CBi/C animals resulted with a longer femur than the control because they were heavier. The response of CBi/L mice validates the hypothesis; since there were no physiological limits imposed, this line had the longest femurs although this was not necessary from the mechanical viewpoint. Response in femur weight was similar to that in length. The source of genetic variance for femoral weight is apparently body weight-dependent and its expression would be conditioned by the soft tissues it must support. Previous studies in other bones also related to the body sustentation system (humerus, scapula, and os-coxae), in adult mice of the four genotypes, showed the same dependence on body weight in their response to selection (DI MASSO et al., 1997b).

The analysis of the regression of femur weight on length suggests firstly that each genotype solved the issue in its own way, secondly that this response is sex-dependent, and thirdly that the genetic determination of both parameters of the allometric relationship is at least partially independent. Genotypes with a high mechanical demand increased their femur mass by increasing the ordinate at origin (CBi+ males and females, and CBi/C males), or by increasing the slope of the relationship (CBi/C females). CBi/L mice, with a low mechanical demand decreased their femur mass by decreasing the ordinate at origin (males), or by decreasing the slope (females). The distinctive behaviour observed both in size and weight is translated, in the antagonically selected lines, in a modification of the femur biomechanic properties (DI MASSO et al, 1997).

A comprehensive description of the underlying regulatory pathway responsible for this dimensional association between body mass and bone function may answer important questions related with the developmental approach of growth studies. An animal model like the one described in this paper would be useful in this sense, as well as to study the dynamics of bone remodeling and bone loss because by disrupting the natural association between total biomass and bone mass, it permits the analysis of variants differing in the biomass supported per unit of skeletal weight.

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Veranstaltungshinweise

34. Kulmbacher Woche

veranstaltet von der Bundesanstalt für Fleischforschung
am 03. bis 05. Mai 1999
Stadthalle Kulmbach

In der Zeit vom 3. Mai (Beginn 10.00 Uhr) bis 5. Mai 1999 findet in der Bundesanstalt für Fleischforschung in Kulmbach die 34. Kulmbacher Woche statt. Das Vortrags- und Posterspektrum umfaßt aktuelle Beiträge zum Schlachtkörperwert, zu einer gesunden Ernährung mit Fleisch, zur Fleischverarbeitung, zu lebensmittelrechtlichen Fragen sowie zur Analytik und zu Nachweismethoden.
Auf dem Programm stehen Vorträge zur Tierhaltung, zur Schlachtkörperqualität und deren Bewertung bei Schweinen, z.B. mit Hilfe der Video-Image-Analyse, oder bei Rindern, zu Qualitätsstandards im Zusammenhang mit dem CMA-Prüfsiegel-Programm. Mehrere Vorträge sind Fragen der Schnellkühlung, den Fetten im Fleisch und speziellen Verarbeitungsproblemen gewidmet. Erwähnt seien auch die Vorträge:

- Klinisch symptomlose VTEC/EHEC-Ausscheider unter dem Personal fleischverarbeitender Betriebe
- BSE-Prophylaxe durch den ELISA-Tiermehl-Test

Ein Lebensmittelrechtliches Kolloquium findet statt und ein Tagungsblock enthält Vorträge zur Dioxinaufnahme über Fleisch und Fleischerzeugnisse, Rückstandsprobleme mit Toxaphen oder eine Methode zur Identifizierung und Differenzierung von Listerien. Zur Fleischforschung und -technologie wird eine Demonstration im Internet angeboten.

Die Anmeldung erfolgt an: Bundesanstalt für Fleischforschung
E.-C.-Baumann-Straße 20
D-95326 Kulmbach

Tel.: 09221/803-269 Fax.:09221/803-244 E-mail: baff@compuserve.com

Anmeldeschluß: 16.04.1999

AfT-Frühjahrssymposium '99

Am 12. und 13. April 1999 findet in Wiesbaden-Naurod das 8. AfT-Frühjahrssymposium zur Thematik „Verdrängte und vernachlässigte Probleme der Tiergesundheit" statt.
Zu den Themen zählen „Schweinepest bei Wildschweinen", „Probleme der ökologischen Rinderhaltung" sowie „Fisch-Wildpopulationen und Fischhaltungen in Deutschland".

Informationen bei: Akademie für Tiergesundheit
Postfach 260164
D-53153 Bonn

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