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THE EFFECT OF SEX ON THE PATTERN OF FAT DEPOSITION IN MICE SELECTED FOR BODY CONFORMATION: AGONISTIC SELECTION

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ABSTRACT

Patterns of fat deposition were investigated in male and female mice divergently selected for body conformation. Selection was carried out with an agonistic criterion between body weight and tail length, in contrast to antagonistic selection previously performed. Within-sex patterns of fat deposition were compared between lines with the logarithmic form of the allometric equation.

Although selected lines were significantly different in body weight, no difference in adult fat content was found between them. Females of both selected lines showed a non-weight-dependent pattern of fat deposition, as found with antagonistic selection, while males showed a weight dependent pattern for both selection procedures.

Selected females did not differ in mature body fat content whether they were selected for high or low body weight, though in both cases they were fatter than unselected controls. These results are explained in terms of adaptive behaviour related to fitness. A critical degree of fatness would be necessary in females to allow the start of the reproductive cycle.

In contrast, no such response was evident in selected males. They did not differ from controls in adult fat percentage. When selection for body size was performed following the natural correlation between body weight and tail length, selected individuals would be heavier because of being bigger and not fatter. This would permit more effective exploitation of the source of genetic variance for body weight associated with appetite, avoiding that associated with energy partitioning.

Body conformation, as herein described, could be an important trait in selection programs directed to obtain lean animals in livestock production, particularly in pigs.

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INTRODUCTION

Trumper *et al.* (1989) studied the effect of sex on the differential contribution of two recognized sources of genetic variation (appetite and efficiency of energy partitioning) for body weight. Following a model proposed by Hayes and McCarthy (1976), the pattern of fat deposition as a correlated response was investigated in two lines of mice selected for body conformation (Di Masso *et al.*, 1990). These lines were divergently selected against the positive correlation between body weight and tail length (antagonistic index selection), line CBi/C being selected for increased 7-week body weight and decreased tail length while line CBi/L was selected for decreased 7-week body weight and increased tail length. Tail length is commonly used as an indicator of skeletal length (Baker and Cockrem, 1970; Reuter, 1976; Hetzel and Nicholas, 1986). Mice of lines CBi/C and CBi/L, with different body lengths, sustained different amounts of biomass, thus showing different body conformations, namely "compact" for CBi/C and "longilineal" for CBi/L. At maturity, in a cross-sectional study, the expected correlated response in total fat weight was observed, since animals selected for high 7-week body weight, as a component of the index, became not only heavier but also fatter as adults.

Using the allometric equation as a dynamic approach, it was shown that the selection criterion did not change the relative rate of fat deposition in males while this character was altered in females. Males showed a weight dependent pattern (similar allometric coefficients) of fat deposition, CBi/C males being fatter than CBi/L not only because they were heavier but also because of their higher relative ranking of fatness at similar carcass weights (different elevations of the regression lines). The particular response observed in females could be explained in terms of pubertal development and the attainment of a particular fat to lean proportion necessary to allow the start of the reproductive cycle.

The aim of this research was to re-evaluate the pattern of fat deposition in relation to sex in mice selected divergently for body conformation based on an agonistic instead of an antagonistic criterion with regard to the correlation between body weight and tail length.

MATERIALS AND METHODS

Two lines of mice were selected for body conformation by means of an index which includes body weight and tail length at seven weeks of age following the positive phenotypic correlation between body weight and tail length (agonistic selection). Line CBi^{+} was selected for increased body weight and tail length while line CBi^{-} was selected

for decreased values of these variables. A detailed description of the selection scheme, including the selective index, is given elsewhere (Di Masso *et al.*, 1990).

Animals from eight to 10 litters were sampled from generation 17 of the selection experiment. The mice were housed at weaning with like-sexed companions in polypropylene cages (32 x 24 x 10 cm) provided with wood shavings for bedding. They were fed *ad libitum* a commercial laboratory chow (Aliper Mouse Chow) and had free access to water.

A random sample of four mice of each sex and line was killed weekly at 3-10 and at 14 weeks of age by etherization and immediately weighed. Food was withheld 12 hours prior to slaughter. They were stored at -20°C until the time of analysis. The mice were roughly chopped into small pieces and then homogenized in a blender. Approximately 10 grams of this homogeneous mixture was used for fat analysis following the extraction technique outlined by Folch *et al.* (1957).

At 24 weeks of age, a random sample of 16 males and 16 females of each line was studied to compare their mature body weights, tail lengths and body fat contents as a percentage of carcass weight.

In order to study fat deposition patterns, regression lines of the form $\ln Y = \ln a + b \ln X$ (where X and Y are body weight and fat weight, respectively lna is the intercept and b is the allometric coefficient) were fitted to allow comparisons at fixed weights. This equation is the double logarithmic form of the allometric relationship $Y = a X^b$ (Huxley, 1932).

Differences among regression coefficients and adjusted means between selected lines within sexes were evaluated using analysis of covariance, while mature body weight, mature tail length and percentage body fat were analyzed by the analysis of variance (Snedecor and Cochran, 1967).

RESULTS

Average mature weights, tail lengths and body fat contents of mice in each sex-line group are given in Table I.

CBi^+ males and females were significantly different from their CBi^- counterparts in terms of body weight ($P < 0.001$) and tail length ($P < 0.001$) resulting in animals not only heavier but also larger at maturity. Within each sex, no significant difference ($P > 0.05$) in fat percentage was found between genotypes. Females were lighter and fatter than males in both lines, though they did not differ in tail length.

When both lines were compared to contemporaneous animals belonging to the control line CBi for adult fat content (CBi males: 7.73 ± 0.40; CBi females: 11.32 ± 0.75), selection resulted in a positively correlated response in females ($P < 0.01$) but not in males ($P > 0.05$).

Table I - Mean live body weight at 24 weeks (g), tail length (cm) and mature body fat content (%) ± standard errors of selected mouse lines.

Sex	Line	n	Body weight	Tail length	Fat percentage
Males	CBi^+	16	47.48 ± 0.98^b	11.55 ± 0.09^b	8.87 ± 0.50^b
	CBi^-	16	28.37 ± 0.61^c	8.71 ± 0.05^c	7.75 ± 0.60^b
Females	CBi^+	16	41.95 ± 0.93^d	11.28 ± 0.10^b	17.78 ± 1.46^c
	CBi^-	16	24.96 ± 0.35^e	8.43 ± 0.08^c	14.99 ± 0.76^c

b,c,d,e Values with different superscript differ at the 0.05 level.

Estimates of the allometric coefficients based on the regression of ln (body fat) on ln (body weight) are shown in Table II. This analysis includes mature mice. The high values of the correlation coefficients indicated that the logarithmic form of the allometric equation gave a good fit for the relationship between fat weight and body weight. No statistical difference was observed in males either in slopes or in elevations of the straight lines. Females showed a different response as they differed in their slopes ($P < 0.05$); therefore, adjusted means could not be compared. CBi^- females were fatter than CBi^+ at low body weights, but as a consequence of the lower value of their allometric coefficient ($CBi^- = 1.36$; $CBi^+ = 1.68$), the difference in fat content became non-significant by adulthood.

Table II - Allometric coefficients and standard errors ($b \pm S_b$) for body fat and tests of significance of the difference between slopes and between elevations of the regression lines.

Sex	Line	$b \pm S_b$	r	Slope	Elevation
Males	CBi^+	1.08 ± 0.06	0.92	ns	ns
	CBi^-	0.85 ± 0.13	0.76		
Females	CBi^+	1.68 ± 0.14	0.85	*	--
	CBi^-	1.36 ± 0.06	0.95		

* ($P < 0.05$), ns ($P > 0.05$) for the comparisons between lines.

DISCUSSION

Previously, it was shown that divergent index selection for body conformation, selecting antagonistically to the positive correlation between body weight and tail length,

resulted in a correlated response in total and relative body fat at maturity (Trumper *et al.*, 1989). As was expected (Roberts, 1979; Malik, 1984), mice selected for high 7-week body weight as a component of the selective index became heavier and fatter as adults. In contrast with the positive selection for body weight and tail length, there was no such correlation with mature fat content.

CBi^+ and CBi^- females did not differ in mature body fat content independently of whether they were selected for high or low body weight but they differed from controls in being fatter than unselected female mice. This result was expected as a correlated response in CBi^+, since it was selected for high body weight but not in CBi^- which was not. As CBi^- was selected for low body weight, a reduction in adult body fat would be predicted.

Selection changed the relative rate of fat deposition in females as allometric coefficients were significantly different. Females of lines CBi^+ and CBi^- (agonistic selection) did not show the weight dependent pattern of fat deposition as was found for antagonistic selection (CBi/C and CBi/L). Selection of CBi^- females would have favoured animals that consumed less and utilized a relatively higher proportion of metabolizable energy for fat deposition. As females significantly differed in their slopes, adjusted means could not be compared, but the observed values for the ordinates at the origin suggested that CBi^- females were fatter than CBi^+ at younger ages as was seen for CBi/C and CBi/L females. This response could be important for fitness because of the critical degree of fatness necessary to allow the start and maintenance of the reproductive cycle (Frisch, 1980; van der Spuy, 1985).

The allometric approach could explain the difference between antagonistic and agonistic selection observed in females. In the former the relation between slopes and ordinates at the origin resulted in a significant difference in adult body fat percentage (intercepting straight lines) not evident in the latter (convergent straight lines).

Another effect of sex was found. No correlated response was evident in CBi^+ and CBi^- males. They did not differ from controls (CBi) in adult body fat percentage. Although males from both lines were selected divergently for high or low body weight as a component of the selective index, they showed the same degree of fatness as adults. Selection did not change the relative rate of fat deposition in males as their allometric coefficients did not significantly differ. CBi^+ and CBi^- mice (agonistic selection) showed a weight dependent pattern of fat deposition. This result is coincident with that arising from the antagonistic selection experiment and suggests that, in this sex, selection operates almost entirely on variation caused by differences in the rate of food consumption. As males did not differ significantly in their allometric coefficients, adjusted means could be compared and a difference between antagonistic and agonistic criteria became evident. CBi/C and CBi/L differed in the elevations of the regression lines while CBi^+ and CBi^- did not differ. As a consequence, CBi^+ males, which were heavier than CBi^-,

had more absolute body fat content at maturity but this difference disappeared when fat content was expressed as a percentage of body weight.

Although a disruptive selection for body weight was implicit in both agonistic and antagonistic selection and, as body weight was jointly selected with tail length in both cases, animals with different body sizes and with different body conformations were generated. When a high weight was combined with a short skeleton, biomass was distributed in a different way than when a high weight was combined with a long skeleton. In the first case, animals from line CBi/C became more fatty near maturity and in the second case, CBi^{+} mice became larger at maturity without changing the fat percentage. This finding confirms that body weight is partially controlled by factors other than body fat content. Therefore, if selection for body size is performed, taking into account body weight together with a linear measurement of size, the variation associated with appetite would be strongly exploited since positively selected individuals would be required to be heavier because of being larger and not of being fatter.

Eisen (1989) reviewed selection experiments for body composition in rodents, emphasizing the necessity to select animals with a low fat percentage because of the serious consequences that overproduction of fat has for the animal industry. Although various more or less sophisticated strategies (use of non invasive methods of estimating body composition, use of transgenic animals) could be developed with this objective and applied to livestock in the future, it is also true that nowadays body weight is still the most widely used criterion for selecting for growth in animals.

It is probable that body conformation as determined by two quantitative characters easily measurable in living animals, as in the experiments herein described, could be an important trait to be considered when selection programs are carried out with the purpose of obtaining lean animals. In pigs, something similar occurs when body weight and body length are considered together to obtain lean animals. This would be particularly useful in males if the hormone-mediated effect that determines a different response in each sex, as is described in this paper, is common to other species.

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RESUMO

Padrões de deposição de gordura foram investigados em fêmeas e machos de camundongos selecionados de modo divergente para estrutura corporal. A seleção foi feita com um critério agonístico entre

peso corporal e comprimento do rabo, em contraste com a seleção antagonística anteriormente feita. As linhas foram comparadas dentro dos padrões sexuais de deposição de gordura com a forma logarítmica e a equação alométrica.

Entretanto as linhas selecionadas foram significativamente diferentes no peso corporal e nenhuma diferença no conteúdo de gordura dos adultos foi encontrada entre eles. Fêmeas de ambas as linhas selecionadas mostraram um padrão de deposição de gordura não dependente de peso, como encontrado com seleção antagonística, enquanto machos mostraram um padrão dependente de peso para ambos os procedimentos de seleção.

Fêmeas selecionadas não diferiram em termos de conteúdo de gordura no corpo adulto se selecionadas tanto para peso corporal alto ou baixo, entretanto ambas eram mais gordas do que os controles não selecionados. Estes resultados são explicados em termos de comportamento adaptivo, relacionado com aptidão. Um grau crítico de gordura seria necessário em fêmeas para permitir o início do ciclo reprodutivo.

Em contraste, nenhuma resposta correlacionada foi evidente em machos relacionados. Eles não diferiram dos controles em termos de porcentagem de gordura do adulto. Quando a seleção para tamanho corporal é feita de acordo com uma correlação natural entre peso corporal e comprimento do rabo, indivíduos selecionados seriam mais pesados porque seriam maiores e não mais gordos. Isto permitiria uma exploração mais efetiva da fonte de variância genética para peso corporal associado ao apetite, evitando a associação com partição.

A conformação do corpo, como descrito neste trabalho, pode ser um fator importante em programas de seleção para obter indivíduos menos pesados em produção de animais, especialmente porcos.

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