

# Carcass composition, bone mechanical properties, and meat quality traits in relation to growth rate in rabbits<sup>1</sup>

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**ABSTRACT:** The objective of this study was to characterize correlated responses in carcass composition, bone mechanical properties, and meat quality indicators to divergent selection for growth rate. Rabbits from low (LOW) or high (HIGH) lines divergently selected over five generations on 63-d BW and a control group (CONT) were used. Rabbits were slaughtered at an average BW of 2,306 ± 65 g, corresponding to 63, 58, or 52 d of age in LOW (n = 41), CONT (n = 43), and HIGH (n = 44) groups, respectively. Postweaning ADG and G:F increased ( $P < 0.001$ ) in the order LOW < CONT < HIGH groups. The lengths of the tibia and femur in rabbit legs decreased ( $P < 0.001$ ) with increasing growth rate. Tibia and femur bone intrinsic stiffness, as assessed by a three-point flexure test, followed the order ( $P < 0.001$ ) of HIGH < CONT < LOW groups. At the same BW, HIGH rabbits and CONT rabbits showed many similarities for dressing percent, carcass composition, and color and chemical composition of muscles or meat parts. In contrast, carcass yield and the relative proportion of hind part were 3% greater ( $P < 0.01$ ) in LOW rabbits than in CONT and HIGH rabbits. The meat-to-bone ratio in the hind leg was 11% greater ( $P$

< 0.001) in the LOW group compared with the CONT and HIGH groups. Yellow color index and moisture content in LM, a fast-twitch glycolytic muscle, were lower ( $P < 0.05$ ) in LOW rabbits than in HIGH rabbits, but ultimate pH, WHC, and cooking loss did not differ between the two growth-selected lines. Ultimate pH in semitendinosus, a mixed slow- and fast-twitch oxidoglycolytic muscle, was less ( $P < 0.001$ ) in HIGH rabbits than in CONT and LOW rabbits. However, lactate dehydrogenase and isocitrate dehydrogenase activities in this muscle (n = 21 per group), assessed at the time of slaughter as markers of glycolytic and oxidative capacities, respectively, did not differ among groups. Growth rate did not modify mean cross-sectional area and type frequency of myofibers in semitendinosus muscle. Finally, Warner-Bratzler shear force and total energy needed to achieve rupture did not differ among groups in semitendinosus muscle (n = 21 per group), whereas they were the least ( $P < 0.001$ ) in LM (n = 128) from HIGH rabbits. Results from this study indicate that improvement of growth rate by selection has little effect in rabbit carcass and meat quality traits.

Key Words: Bone Resistance, Carcass Composition, Growth Rate, Meat Quality, Muscle Fibers, Rabbits

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## Introduction

Selection for growth rate is commonly practiced in rabbit sire lines. Selection increases all weights along the growth curve (Blasco et al., 2003). Because carcass weight is fixed by the market, selection for an improved

growth rate results in less mature animals, as expressed as weight divided by adult BW. The importance of examining the results of selection in relation to maturity degree was accentuated by Taylor (1985), who concluded that most of the phenotypic responses observed in growth-selected animals have been achieved as a consequence of change in adult size; however, a part of the phenotypic variance is truly genetic. Divergently selected lines may provide a model of both genetic and biological relevance for analyzing complex quantitative responses. Because rabbit meat is found both as a whole or cut-up carcass and processed ready products, classical attributes of quality for both carcass and meat need to be considered. Bone resistance recently has been considered as another quality factor (Lebas et al., 1998;

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Xiccato et al., 1999) for the commercialization of retail cuts and mechanically deboned meats. The frequency of leg bone breaking during carcass handling has been estimated to be approximately 10% of the slaughtered animals. An increased growth rate may be associated with lower bone-bending resistance in chicks (Leterrier and Nys, 1992). In a previous study, we investigated responses to growth rate in rabbits divergently selected for 63-d BW and a control group, slaughtered at a constant age but different BW (Larzul et al., 2005). We showed that differences in growth rates between lines were of genetic origin, and a positive genetic correlation was found between carcass fat proportion and 63-d BW. Meat pH was not affected by selection, and minor modifications were noted for raw meat texture. The present study was aimed at evaluating the effects of growth rate on extended quality traits, including bone properties, in the same three lines slaughtered at a constant BW.

## Materials and Methods

### *Animals and Management*

Two selection lines were formed from a commercial heavy sire line (Grimaud Frères, Roussay, France), introduced after hysterectomy of the females on an INRA (Institut National de la Recherche Agronomique) experimental herd (SELAP, Toulouse, France). They were reared in compliance with French regulations for humane care and use of animals in research. During five generations, rabbits were divergently selected on their breeding value for a high (**HIGH**) or a low (**LOW**) 63-d BW, as described by Larzul et al. (2005). Cryopreserved embryos of founders were thawed and implanted in does belonging to Generation 4 to produce parents of the control (**CONT**) group. At Generation 5, does were inseminated within 6-d intervals between each line, in the following order: LOW, CONT, and HIGH lines. A total of 195 rabbits, 65 of each group, were weaned at approximately 30 d of age. They were individually caged and given ad libitum access to a commercial diet (barley and wheat as the primary grains, alfalfa hay as the fiber source, beet pulp, soybean and sunflower meals) formulated (DM basis) for growing rabbits (16.5% CP, 3.0% fat, 15.8% crude fiber, 7.8% ash, 10.5 MJ of ME/kg). The day before slaughter, 67 males and 61 females from either the LOW line (n = 41), CONT group (n = 43), or HIGH line (n = 44) were finally retained among the 195 rabbits available at weaning to minimize individual BW variation at slaughter.

### *Growth Performance and Carcass Measurements*

Body weight changes and individual feed consumption were recorded each week from weaning to slaughter for the calculation of ADG and G:F, respectively. At  $2,306 \pm 65$  g BW, rabbits were transported in two batches (n = 63 and 65, respectively) at 3-d intervals to the experimental slaughterhouse of INRA at Toulouse,

France (15 min transport duration). They were slaughtered without prior fasting in compliance with French national regulations for commercial slaughtering. Hot carcass (minus blood, lungs, genital organs, viscera, urinary bladder, and skin) was weighed. The percentages of skin and viscera were calculated as follows: (weight/preslaughter BW)  $\times$  100. After 24 h of chilling, the weighed carcass was divided according to the norms of the World Rabbit Scientific Association (Blasco and Ouhayoun, 1996). Dressing percent ([chilled carcass weight/preslaughter BW]  $\times$  100%), and percentages ([weight/chilled carcass weight]  $\times$  100%) of perirenal fat, interscapular fat, and fore- (from atlas vertebra to the seventh thoracic vertebra), intermediate- (from the seventh thoracic vertebra to the sixth lumbar vertebra), and hind- (from the sixth lumbar vertebra) parts were calculated in a subset of carcasses (n = 20, 22, and 23 in the LOW, CONT, and HIGH groups, respectively). Fore parts were vacuum-packed and frozen at  $-20^{\circ}\text{C}$  until the chemical composition was determined. The left hind legs (n = 65) were separated, weighed, vacuum-packed, and frozen at  $-20^{\circ}\text{C}$  for the estimation of the muscle-to-bone ratio. The left intermediate parts were separated, vacuum-packed, and frozen at  $-20^{\circ}\text{C}$ , for the estimation of water-holding capacity (**WHC**). The right intermediate parts and the hind legs of all carcasses (n = 128) were kept one more day at  $4^{\circ}\text{C}$ . At 48 h post-mortem, the right hind legs of carcasses were vacuum-packed after removal of selected muscles and frozen at  $-20^{\circ}\text{C}$  until the bone flexure test.

### *Muscle Samples: Collection and Preparation*

Two morphologically and functionally distinct skeletal muscles were selected in a subset of the left carcasses within 15 min of slaughter: the LM adjacent to the fifth and sixth lumbar vertebra levels (n = 20, 22, and 23 in the LOW, CONT, and HIGH groups, respectively) and the entire semitendinosus (**ST**; n = 21 per group). All epimysial connective tissue and intermuscular fat depots were trimmed and discarded. Two slices of ST were taken in the mid-belly of the muscle; a slice was immediately frozen in liquid  $\text{N}_2$  for enzymatic measurements, and another slice was cooled at  $4^{\circ}\text{C}$  during 1 h after removal for determination of muscle cross-sectional area. Two samples prepared following fiber direction (200 mg each) were taken at fixed points in the ST, one in the red deep part and one in the superficial white part, for evaluation of myofiber characteristics. They were restrained on flat sticks and frozen in 2-methylbutane cooled with liquid  $\text{N}_2$ . The LM samples and the remaining mid-part of ST were cut into small pieces and frozen in liquid  $\text{N}_2$  for biochemical evaluation. All samples were stored at  $-70^{\circ}\text{C}$  until further processing. At 48 h post-mortem, LM (first to sixth lumbar vertebra levels) and ST were excised from all or a subset of right carcasses (n = 21 per group), respectively, and processed for rheological measurements.

### Bone Mechanical Testing

Right legs were thawed to room temperature, and tibia and femurs were removed and weighed. Finally, only 123 samples could be considered. The bones were submitted to a three-point flexure test conducted with a universal testing machine (Synergie 200; MTS, Eden Prairie, MN). The distance between the two fulcrum points supporting the bones was 30 mm and a load was applied at 5 mm/min. Lengths, inside (B and D) and outside (b and d) diameters at the point of loading, both perpendicular and parallel to the direction of the applied force, were measured using a dial caliper ( $\pm 0.02$  mm). The area moment of inertia (**MI**), which is an estimate of bone distribution assuming that the bone shape is similar to that of an elliptical hollow tube (Crenshaw et al., 1981), was calculated according to the following formula:

$$MI = 0.0491 (BD^3 - bd^3)$$

Yield force, ultimate force, and stiffness (slope of the elastic part) were collected from the load deformation curve, whereas bone stress as yield force per unit of bone area, and modulus of elasticity as a measure of the degree of rigidity of the bone, were calculated according to formula reported by Patterson et al. (1986).

### pH and Meat Color Measurements

At 24 h postmortem, meat color was assessed on a freshly exposed cut surface of LM (seventh lumbar vertebra) and on the surface over the biceps femoris (**BF**) of all carcasses ( $n = 128$ ). A Minolta CR-300 chromameter (Minolta, Osaka, Japan) was set to the  $L^*$  (lightness),  $a^*$  (redness),  $b^*$  (yellowness) scale. Values corresponded to the average of three measurements at each point. The pH was then obtained from the LM (adjacent to the seventh lumbar vertebra level) and at the surface over the BF with a combined glass penetrating electrode (Ingold, Mettler Toledo, Greifensee, Switzerland) and a portable pH meter (WTW 340i, Weilheim, Germany). After 24 h of chilling, pH can be considered to have reached its ultimate value (Hulot and Ouhayoun, 1999); however, pH was measured in ST only at 48 h postmortem, after rheological measurements had been made ( $n = 21$  per group). Due to heterogeneity between red and white portions, ST was crushed in a solution of sodium iodo-acetate (5 mM; 1:9 wt/vol) before pH was measured using the apparatus described above.

### Properties of Cooked Meat

The left hind leg was thawed for 24 h at 4°C, weighed, and cooked at 80°C for 2.5 h in a wet oven. Cooking loss was calculated as the ratio of cooked to fresh weight. Muscle-to-bone ratio in the hind leg was then calculated as the ratio of deboned cooked meat to bone weights multiplied by 100, and was used as an indicator of the

lean-to-bone ratio in rabbit carcasses (Blasco and Ouhayoun, 1996). After thawing the left intermediate parts (2 h in running water), a sample of LM was weighed (approximately 4 g; first to third lumbar vertebra), vacuum-packed, and cooked in a water bath (80°C) for 40 min. Cooking loss in LM was assessed as described above for the hind leg. Water-holding capacity was estimated by centrifuging raw or cooked LM portions for 10 min at  $1,500 \times g$ , and determining the residual water by drying the sample at 103°C overnight, according to Castellini et al. (1998). The WHC was calculated with the following equation (multiplied by 100):

$$WHC =$$

$$\frac{(\text{weight after centrifugation} - \text{weight after drying})}{\text{initial muscle weight}}$$

### Chemical Analyses

Whole left fore-part (approximately 100 g) and LM sample (approximately 3 g; mid-portion) were ground to a smooth paste in a domestic mincer, and moisture content was measured from the weight loss of samples dried overnight at 103°C (AOAC, 1990). Total lipid contents in LM and ST (approximately 4 g) were determined after extraction with methanol/chloroform (Folch et al., 1957).

### Warner-Bratzler Shear Test

Due to the high heat solubility of i.m. collagen in rabbits (Combes et al., 2004), shear tests allow a better differentiation between age groups when performed on raw than on cooked rabbit meat (Cauquil et al., 2001). An entire cross-section in the mid-portion of right LM was photographed, and muscle cross-section area was measured by image analysis ( $n = 128$ ). Considering its small size, right ST was kept whole ( $n = 21$  per group). Muscles were sheared perpendicular to myofiber direction with a Warner-Bratzler device adapted to a universal testing machine (Synergie 200) and a crosshead speed of 100 mm/min. The parameters from the force displacement curve were shear force applied at maximum (**F<sub>m</sub>**) and energy at maximum. The total energy necessary to break the sample was calculated as the area under the force displacement curve, and was assumed to be representative of toughness. Stiffness was assessed by calculating the ratio of **F<sub>m</sub>** to displacement to **F<sub>m</sub>**. Stress was calculated as follows (Salé, 1971):

$$\text{Stress} = 0.05 [F_m/MCSA]$$

where MCSA is the cross-sectional area of the entire muscle.

### Histological Analyses

Histochemistry was performed on transverse serial cross-sections of left ST samples, cut in a cryostat at

**Table 1.** Performance by rabbits from weaning to slaughter as influenced by growth rate<sup>a</sup>

Variable	LOW	CONT	HIGH	SEM
No. of rabbits	41	43	44	—
Weaning BW, g	726 <sup>c</sup>	795 <sup>d</sup>	903 <sup>e</sup>	9
Final BW, g	2,308	2,311	2,300	10
Final age, d <sup>b</sup>	63.3	58.0	52.2	—
ADG, g	47.2 <sup>c</sup>	55.0 <sup>d</sup>	65.2 <sup>e</sup>	0.5
Feed consumption (as-fed basis), g/d	150.3 <sup>c</sup>	155.3 <sup>d</sup>	171.8 <sup>e</sup>	35
Days on feed	33.5	27.5	21.5	—
G:F, g/kg	314 <sup>c</sup>	354 <sup>d</sup>	379 <sup>e</sup>	3

<sup>a</sup>Rabbits were divergently selected for a low (LOW) or a high (HIGH) 63-d BW, and the control growth rate group (CONT) comprised rabbits derived from cryopreserved embryos obtained from founder rabbits.

<sup>b</sup>Rabbits were slaughtered at 104 and 107 d, 98 and 101 d, or 92 and 95 d after insemination, for LOW, CONT, and HIGH groups, respectively.

<sup>c,d,e</sup>Within a row, least squares means without a common superscript letter differ,  $P < 0.05$ .

–20°C (2800 Frigocut, Reichert-Jung, Francheville, France). A section (14 µm thick) was stained with azorubin for reference. Mean cross-sectional area of myofibers was determined from selected fields (170 to 220 fibers per field), three in each part, after interfiber network extraction using a macro program developed on an image analysis system (Optimas 6.5, Media Cybernetics, Silver Spring, MD). The total number of myofibers was estimated by extrapolation from the number of fibers counted over the six fields of known size, and from the muscle cross-sectional area measured on the ST slice with a programmable planimeter (Hitashi Siko, Tokyo, Japan). A serial section (10 µm thick) was stained using conventional mATPase histochemistry after preincubation at pH 4.35 to identify Types I, IIA, and IIB fibers (Brooke and Kaiser, 1970). The relative percentage of each fiber type was determined on the basis of 300 to 400 fibers per field selected, three in each part, using a projection microscope (Reichert-Jung Visopan, Vienna, Austria).

#### Metabolic Enzyme Activities

Activities of lactate dehydrogenase (**LDH**) and isocitrate dehydrogenase (**ICDH**) were used as markers of glycolytic metabolism and global oxidative capacity (tricarboxylic cycle), respectively. Briefly, the ST slice from left carcasses was homogenized and sonicated in seven volumes (wt/vol) of ice-chilled 0.1 M phosphate buffer (pH 7.5) containing 2 mM EDTA. After centrifugation at  $1,700 \times g$  for 15 min at 4°C, the supernatant fraction was collected and immediately used for analysis. Enzyme activities were measured ( $\mu\text{mole of degraded substrate} \cdot \text{min}^{-1} \cdot \text{g fresh tissue}^{-1}$ ) by continuous kinetics at 340 nm using a spectrophotometer (Uvikon XS, UVK-Lab, Paris, France), after addition of pyruvic acid and the reduced form of NADH for LDH, and of DL-isocitrate and NADP for ICDH, respectively, as previously described (Bergmeyer and Bernt, 1974; Briand et al., 1981).

#### Statistical Analyses

Data were submitted to ANOVA using the SAS software (SAS Inst. Inc., Cary, NC), with growth rate

groups (three levels), slaughter series (two levels), and sex (two levels) as main effects, and deviation to the average preslaughter BW as the covariate. Because they were not significant, deviation to the average BW and sex were removed from the final analyses. First-order interactions also were tested but not retained in the final model because they were never significant. Least squares means values for the effect of growth rate groups were compared using the PDIFF statement of the GLM procedure with a Tukey-Kramer multiple comparison adjustment.

## Results

### Performance and Carcass Traits

At weaning, BW was decreased by 69 g in LOW rabbits compared with CONT rabbits (Table 1), whereas it was increased by 108 g in HIGH rabbits compared with CONT rabbits ( $P < 0.001$ ). As expected, LOW rabbits had a 14% lower postweaning ADG compared with controls, and a 28% lower ADG compared with HIGH rabbits ( $P < 0.001$ ). This gave rise to a 5 to 11 d increase in slaughter age in the former group compared with CONT and HIGH animals, respectively. Rabbits of the LOW group consumed 3% less food per day than CONT rabbits, and the difference reached 12% between the two divergent lines ( $P < 0.001$ ). Increasing ADG in HIGH rabbits caused a 7% increase in G:F compared with CONT rabbits, and the difference in feed efficiency reached 22% when HIGH rabbits were compared with LOW rabbits ( $P < 0.001$ ).

Asymmetrical responses to selection were observed for carcass conformation, with responses in the LOW group only (Table 2). Carcass weight and dressing percent were higher ( $P < 0.001$ ) in LOW rabbits than in the two other groups. This resulted mainly from a lower development of viscera (–7.4%;  $P < 0.001$ ) in LOW rabbits than in CONT rabbits and HIGH animals, whereas hind part proportion was increased by 3% ( $P = 0.003$ ) in the former group compared with others. Relative proportions of other carcass parts and body fatness did

**Table 2.** Carcass measurements of rabbits as influenced by growth rate<sup>a</sup>

Variable	LOW	CONT	HIGH	SEM
No. of rabbits	41	43	44	
Hot carcass weight, g	1,389 <sup>c</sup>	1,365 <sup>c</sup>	1,339 <sup>d</sup>	7
Viscera, % BW	16.2 <sup>c</sup>	17.4 <sup>d</sup>	17.6 <sup>d</sup>	0.2
Skin, % BW	19.8 <sup>c</sup>	19.2 <sup>d</sup>	19.5 <sup>cd</sup>	0.2
No. of rabbits	20	22	23	
Chilled carcass weight, g	1,358 <sup>c</sup>	1,314 <sup>d</sup>	1,313 <sup>d</sup>	7
Dressing percent	58.6 <sup>c</sup>	56.8 <sup>d</sup>	56.7 <sup>d</sup>	0.2
Meat part proportion, % <sup>b</sup>				
Fore part	34.1	34.3	34.2	0.2
Intermediate part	17.2	16.8	16.7	0.2
Hind part	31.4 <sup>c</sup>	30.3 <sup>d</sup>	30.3 <sup>d</sup>	0.2
Fat proportion, % <sup>b</sup>				
Perirenal	1.76	1.76	1.64	0.08
Scapular	0.52	0.55	0.56	0.03
Muscle-to-bone ratio	7.1 <sup>c</sup>	6.4 <sup>d</sup>	6.3 <sup>d</sup>	0.1

<sup>a</sup>Rabbits were divergently selected for a low (LOW) or a high (HIGH) 63-d BW, and the control growth rate group (CONT) were rabbits derived from cryopreserved embryos obtained from founder rabbits.

<sup>b</sup>Expressed relative to chilled carcass weight.

<sup>c,d</sup>Within a row, least squares means without a common superscript letter differ,  $P < 0.05$ .

not differ among groups. Finally, the muscle-to-bone ratio was 11% higher ( $P < 0.001$ ) in LOW rabbits than in the two other groups.

### Bone Properties

As shown in Table 3, bone wet weights did not differ according to growth rate. Bone lengths ranked in the following order: HIGH, CONT, and LOW groups ( $P < 0.001$ ). The LOW rabbits displayed the lowest MI for the femur ( $P < 0.001$ ) because of a low external bone diameter, whereas differences between lines for MI in tibia did not reach significance level ( $P = 0.06$ ). Bone-

specific responses to growth rates were shown for most traits (Table 3), except stiffness, which decreased ( $P < 0.001$ ) with increasing growth rate for both bones. Yield and ultimate forces in femurs were 13 and 9% less ( $P < 0.005$ ), respectively, in LOW rabbits than CONT rabbits, whereas both forces in the tibias were greatest in LOW rabbits ( $P < 0.005$ ). The modulus of elasticity, as an indication of basic material elasticity independent of geometry, was the highest in the femurs of LOW rabbits, whereas it did not differ among groups in the tibia. Regardless of the bone, stress, as a measure of force per unit of area, did not differ among the three groups.

**Table 3.** Bone shape and mechanical properties of the femur and tibia of rabbits as affected by growth rate<sup>a</sup>

Variable	Bone	LOW	CONT	HIGH	SEM
No. of rabbits	—	39	43	41	—
Weight, g	Femur	10.5	10.8	10.6	0.1
Length, mm	Femur	78 <sup>d</sup>	76 <sup>c</sup>	74 <sup>b</sup>	0.3
Moment of inertia, mm <sup>4</sup>	Femur	93 <sup>b</sup>	120 <sup>c</sup>	114 <sup>c</sup>	4
Yield force, kg	Femur	18.4 <sup>b</sup>	21.1 <sup>c</sup>	21.3 <sup>c</sup>	0.5
Ultimate force, kg	Femur	26.1 <sup>b</sup>	28.7 <sup>c</sup>	27.0 <sup>bc</sup>	0.6
Stress, kg/mm <sup>2</sup>	Femur	5.0	4.8	4.9	0.2
Stiffness, kg/mm	Femur	29.7 <sup>d</sup>	27.2 <sup>c</sup>	24.9 <sup>b</sup>	0.7
Elastic modulus, kg/mm <sup>2</sup>	Femur	188 <sup>c</sup>	135 <sup>b</sup>	128 <sup>b</sup>	6
No. of rabbits	—	39	43	41	—
Weight, g	Tibia	8.2	8.4	8.3	0.1
Length, mm	Tibia	86 <sup>d</sup>	84 <sup>c</sup>	81 <sup>b</sup>	0.3
Moment of inertia, mm <sup>4</sup>	Tibia	52	47	43	3
Yield force, kg	Tibia	26.8 <sup>c</sup>	23.9 <sup>b</sup>	23.7 <sup>b</sup>	0.7
Ultimate force, kg	Tibia	31.2 <sup>c</sup>	29.2 <sup>b</sup>	27.9 <sup>b</sup>	0.6
Stress, kg/mm <sup>2</sup>	Tibia	11.1	10.4	10.7	0.3
Stiffness, kg/mm	Tibia	40.5 <sup>d</sup>	36.8 <sup>c</sup>	33.8 <sup>b</sup>	0.7
Elastic modulus, kg/mm <sup>2</sup>	Tibia	487	465	458	17

<sup>a</sup>Rabbits were divergently selected for a low (LOW) or a high (HIGH) 63-d BW, and the control growth rate group (CONT) were rabbits derived from cryopreserved embryos obtained from founder rabbits.

<sup>b,c,d</sup>Within a row, least squares means without a common superscript letter differ,  $P < 0.05$ .

**Table 4.** Meat quality indicators in muscles and carcass parts of rabbits as affected by growth rate<sup>a</sup>

Variable	Muscle	LOW	CONT	HIGH	SEM
No. of rabbits	—	41	43	44	—
Ultimate pH	Biceps femoris	6.01	6.02	5.96	0.02
CIE L*	Biceps femoris	54.9	54.8	55.1	0.4
CIE a*	Biceps femoris	3.9	4.4	4.1	0.3
CIE b*	Biceps femoris	3.8 <sup>b</sup>	4.6 <sup>c</sup>	4.5 <sup>c</sup>	0.2
Ultimate pH	LM	5.74	5.74	5.74	0.01
CIE L*	LM	58.7 <sup>b</sup>	59.1 <sup>bc</sup>	60.3 <sup>c</sup>	0.4
CIE a*	LM	3.4	4.0	4.1	0.2
CIE b*	LM	4.2 <sup>b</sup>	5.0 <sup>bc</sup>	5.6 <sup>c</sup>	0.2
No. of rabbits	—	20	22	23	—
Lipid, % fresh tissue	LM	1.2	1.1	1.2	0.03
Moisture, %	LM	74.9 <sup>b</sup>	75.1 <sup>bc</sup>	75.3 <sup>c</sup>	0.1
WHC <sub>raw</sub>	LM	59.9	60.4	59.4	0.6
WHC <sub>cooked</sub>	LM	56.7 <sup>b</sup>	58.3 <sup>c</sup>	58.0 <sup>bc</sup>	0.4
Cooking loss, %	LM	34.2	34.0	34.6	0.4
Moisture, %	Fore part	63.7 <sup>b</sup>	64.3 <sup>bc</sup>	65.1 <sup>c</sup>	0.3
Cooking loss, %	Hind part	24.7	24.6	23.5	0.8
No. of rabbits	—	21	21	21	—
Ultimate pH	Semitendinosus	6.13 <sup>c</sup>	6.10 <sup>c</sup>	6.02 <sup>b</sup>	0.02
Lipid, % fresh tissue	Semitendinosus	2.1	2.3	2.2	0.1

<sup>a</sup>Rabbits were divergently selected for a low (LOW) or a high (HIGH) 63-d BW, and the control growth rate group (CONT) were rabbits derived from cryopreserved embryos obtained from founder rabbits. CIE L\* = a measure of lightness, with a larger number indicating a lighter color; CIE a\* = red (+) to green (–) color scale; CIE b\* = yellow (+) to blue (–) color scale; WHC<sub>raw</sub> = water-holding capacity of raw meat; WHC<sub>cooked</sub> = water-holding capacity of cooked meat.

<sup>b,c</sup>Within a row, least squares means without a common superscript letter differ,  $P < 0.05$ .

### Meat Quality Traits

The indicators of meat quality are presented in Table 4. Ultimate pH in ST was less in HIGH rabbits than in LOW and CONT rabbits ( $P < 0.001$ ), whereas pH did not differ among groups in BF ( $P = 0.11$ ) or LM ( $P = 0.88$ ). The L\* index was lower in the LM section of LOW rabbits than in HIGH rabbits ( $P = 0.02$ ), whereas CONT rabbits had an intermediate value. In contrast, L\* value did not differ among groups ( $P = 0.81$ ) when measured over the BF surface. Whatever the muscle, the b\* index was less ( $P < 0.01$ ) in LOW rabbits than in HIGH group, whereas redness (a\*) did not differ among groups.

Neither WHC of raw meat or cooking loss differed according to growth rate. The WHC of cooked LM was slightly lower in LOW rabbits than in CONT animals ( $P < 0.05$ ), but it did not differ significantly between the two selected lines. Moisture percent was lower in LM ( $P = 0.004$ ) and carcass fore part ( $P = 0.02$ ) of LOW rabbits than of HIGH rabbits, whereas CONT rabbits exhibited intermediate values. Conversely, muscle fat content in both LM and ST did not differ between the three groups.

### Rheological and Histological Properties of Muscles

Shear force, energy at maximum, and total energy needed to achieve rupture in LM were lower ( $P < 0.05$ ) in HIGH rabbits than in the two other groups, whereas LOW rabbits and controls displayed similar rheological

characteristics (Table 5). Stress value was slightly lower in HIGH rabbits than in controls, but there was no significant difference between the two divergent lines. Stiffness did not differ among growth rate groups. Warner-Bratzler measurements in ST muscle did not differ among groups. Similarly, total number, mean cross-sectional area, and type frequency of the myofibers in ST did not differ between the three groups (Table 6). In addition, the aerobic capacity, as indicated by the activity of ICDH, and the anaerobic capacity, as indicated by the activity of LDH, did not differ in ST muscles of either group.

### Discussion

It is difficult to make a fair comparison on carcass and meat quality traits between divergent growth-selected lines because animals differing in asymptotic size do not have the same degree of maturity at a fixed BW or the same physiological age at a constant calendar age, respectively (Taylor, 1985). In a previous experiment (Larzul et al., 2005), we showed that differences in growth rate between the LOW, HIGH, and CONT rabbit lines were of genetic origin; however, minor modifications were observed on classically used indicators of meat quality in rabbits slaughtered at a fixed age. Because carcass weight is fixed by the market, comparing animals at the same BW (i.e., taking into account differences in age at slaughter) is of greater interest for rabbit meat production. Correlated effects of selection for

**Table 5.** Warner-Bratzler shear measurements in muscles of rabbits as affected by growth rate<sup>a</sup>

Variable	Muscle	LOW	CONT	HIGH	SEM
No. of rabbits	—	41	43	44	—
Maximum shear force, kg	LM	3.5 <sup>b</sup>	3.4 <sup>b</sup>	2.9 <sup>c</sup>	0.1
Energy at maximum, mJ	LM	283 <sup>b</sup>	271 <sup>b</sup>	222 <sup>c</sup>	9
Total energy, mJ	LM	735 <sup>b</sup>	705 <sup>b</sup>	590 <sup>c</sup>	14
Stiffness, kg/cm	LM	2.2	2.2	2.0	0.05
Stress, kg/cm <sup>2</sup>	LM	0.39 <sup>bc</sup>	0.41 <sup>b</sup>	0.37 <sup>c</sup>	0.01
No. of rabbits	—	21	21	21	—
Maximum shear force, kg	Semitendinosus	3.8	3.8	3.6	0.2
Energy at maximum, mJ	Semitendinosus	143	155	130	8
Total energy, mJ	Semitendinosus	399	394	365	14
Stiffness, kg/cm	Semitendinosus	5.9	5.6	5.8	0.3
Stress, kg/cm <sup>2</sup>	Semitendinosus	0.81	0.80	0.80	0.04

<sup>a</sup>Rabbits were divergently selected for a low (LOW) or a high (HIGH) 63-d BW, and the control growth rate group (CONT) were rabbits derived from cryopreserved embryos obtained from founder rabbits.

<sup>b,c</sup>Within a row, least squares means without a common superscript letter differ,  $P < 0.05$ .

growth rate cannot be estimated solely by comparing rabbits of different ages within a given lot because phenotypic correlations are scarcely similar to genetic correlations. Therefore, comparing divergently selected lines at a constant BW also may be a relevant biological model to understanding tissue development in relation to growth rate.

As a consequence of mass selection, the rabbits of the HIGH and LOW groups were heavier or lighter, respectively, than controls at weaning. In agreement, Blasco et al. (2003) showed that rabbits selected for an increased growth rate had a higher live BW along the whole growth curve than rabbits from a cryo-preserved control line compared at the same age. The same rank order of LOW < CONT < HIGH rabbits for postweaning ADG and G:F matched with the negative genetic corre-

lation reported between ADG and feed conversion ratio in rabbits (Moura et al., 1997; Piles et al., 2004). A difference of 694 g for adult size between LOW and HIGH male rabbits has been previously estimated after three generations of selection (Gondret et al., 2002). Therefore, the current findings of higher carcass yield, hind part proportion, and muscle-to-bone ratio in LOW rabbits compared with HIGH rabbits were consistent with general patterns of body composition in relation to maturity degree (Taylor, 1985). Nonetheless, Pla et al. (1998) observed that meat-to-bone ratio was similar between breeds selected for high growth or litter size, respectively, slaughtered at a same BW.

Similar fattening percent in chilled carcasses among our three growth-rate groups were somewhat surprising because the trend is generally toward more body

**Table 6.** Histological characteristics and enzyme activities in semitendinosus muscle of rabbits<sup>a,b</sup>

Variable	LOW	CONT	HIGH	SEM
No. of rabbits	21	21	21	—
Total fiber number	76,708	75,692	79,949	1,673
Myofiber cross-sectional area, $\mu\text{m}^2$	2,883	3,036	2,885	66
Histoenzymology in deep part, % <sup>c</sup>				
I	15.9	14.9	17.3	1.2
IIA	15.2	16.4	16.1	1.0
IIB	68.9	68.7	66.6	1.7
Histoenzymology in superficial part, % <sup>c</sup>				
I	1.0	0.7	1.2	0.3
IIA	5.4	5.0	6.6	0.6
IIB	93.6	94.3	92.2	0.8
LDH, $\mu\text{mol substrate degraded}\cdot\text{min}^{-1}\cdot\text{g fresh muscle}^{-1}\text{d}$	1,113	1,106	984	57
ICDH, $\mu\text{mol substrate degraded}\cdot\text{min}^{-1}\cdot\text{g fresh muscle}^{-1}\text{e}$	11.7	12.3	11.6	0.5

<sup>a</sup>Rabbits were divergently selected for a low (LOW) or a high (HIGH) 63-d BW, and the control growth rate group (CONT) were rabbits derived from cryopreserved embryos obtained from founder rabbits.

<sup>b</sup>All traits under study did not differ between growth rate groups.

<sup>c</sup>Conventional mATPase typing, determined either in the red deep part or in the white superficial part of the muscle.

<sup>d</sup>LDH = lactate dehydrogenase.

<sup>e</sup>ICDH = isocitrate dehydrogenase.

fat in more mature animals (Taylor, 1985). This may have resulted from a lower daily food consumption in LOW rabbits than in HIGH animals. Alternatively, down-selection for 63-d BW may have lowered the rate of lipid deposition in tissues because a positive genetic correlation between ADG and carcass fat proportion has been described in rabbits (Larzul et al., 2005). We did not observe any phenotypic responses to selection for an improved BW in carcass composition compared with a cryo-preserved group. This observation was similar to that obtained in the same lines slaughtered at a fixed age (Larzul et al., 2005). In addition, Piles et al. (2000) postulated that the lower maturity degree of rabbits selected for a high growth rate would not lead to appreciable changes in carcass composition, except carcass fatness, when compared with a control group. Applying the size-scaling theory of Taylor (1985), the lack of difference in carcass merit between HIGH rabbits and their controls suggested that genetic factors could compensate for the known effects of differences in physiological development. Many causes may generate asymmetrical phenotypic responses between divergent lines, as reviewed and discussed by Falconer (1981). Because correlations between litter size and growth rate generally are low in rabbits (see Garreau et al., 2004, for a review), it seems unlikely that a maternal component of the selected trait may be implicated. Therefore, the genetic asymmetry observed in our experiment might be related to some form of genotype  $\times$  environment interaction, inbreeding, or nonlinear relations between traits.

Rabbit bone lengths ranked in the same order than ADG in the current study, probably as a result of correlated difference in age at a same BW (Letierrier and Nys, 1992). Differences for other bone traits were found in slow-growing animals only, with a noticeable exception for stiffness, which decreased with growth rate among the three groups. In pigs, Liu et al. (1999) have shown that an increase in tibia diameter is in proportion to BW, whereas the diameter of femur has greater than proportional growth rate. This finding might explain why there was no difference in tibia MI among the three groups compared at similar BW, whereas the lowest MI for femur was observed in slow-growing rabbits. Considering that flexure forces in femur were lower, but elastic modulus and stiffness were higher in slow-growing rabbits compared with rapid-growing ones, respectively, we suggest that both shape and basic material (mineral reserves) were affected by growth selection in this bone. Conversely, the fact that no change in elastic modulus was evidenced among groups in tibia, despite higher flexure forces and stiffness in LOW rabbits than in HIGH rabbits, suggests that divergent selection for BW was manifested mainly in geometric terms for the tibia. Similarly, Letierrier and Nys (1992) have evidenced higher flexure forces and stiffness of tibiotarsi in slow-growing vs. rapidly growing chicks at the same BW. Considering that the tibia is the main site of bone fracture during slaughtering, it

was suggested that increasing growth rate resulting in decreased intrinsic material stiffness may represent a problem for carcass process quality.

Meat pH affects many meat quality properties, including WHC and color in rabbits (Hulot and Ouhayoun, 1999). Literature data on ultimate pH for various muscles in response to growth selection or growth precocity are controversial, with reports of higher (Pla et al., 1998), lower (Cabanes-Roiron and Ouhayoun, 1994), or the same (Hernandez et al., 1997) value in rapid-growing rabbits compared with rabbits undergoing a slower growth rate. We did not find evidence of any variation in pH for LM or BF among the three groups, but we noted a lower pH in semitendinosus muscle with increasing growth rate. However, no significant changes in the metabolic energy pathway in ST muscle, as measured by enzyme activities, could be found to explain differences in ultimate pH among lines, an observation similar to that reported in chicks (Berri et al., 2001). Postmortem, glycogen is converted to H<sup>+</sup> and lactic acid, resulting in decreased pH. Therefore, one possible reason for such muscle-specific variation in pH may be that the amplitude of increase in the muscle glycogen content following upward growth selection would be higher in ST muscle than in BF and LM, in which glycolytic metabolism is already elevated (Delmas and Ouhayoun, 1990). A decrease in the WHC of the raw meat should be expected in rapid-growing rabbits as a consequence of a low degree of maturity and lower meat fat content (Piles et al., 2000); however, we did not find evidence of any changes in the WHC of raw meat, cooking loss, and muscle fat content among the three groups. In agreement with the findings of Pla et al. (1998), who compared a breed selected for a rapid growth speed and breeds selected on reproductive traits, we also did not find any variation on WHC of cooked meat between the two divergent lines. The reason for the higher WHC of cooked meat in controls than in LOW rabbits remains unexplained, however. Changing animal growth rate by mass selection obviously implies modifications in the age of animals at the same BW. Then, the rank order observed for moisture percentage in rabbit tissues between growth-rate groups may partly be attributed to difference in age at slaughter (Cavani et al., 2000; Hernandez et al., 2004). Comparisons with other studies for meat color are limited. Contrary to our results of darker muscles for slow-growing rabbits compared with rapidly growing ones, Hernandez et al. (1997) found similar L\* value in the same muscles between rabbit breeds with different growth rates. The reasons for a lower yellow index of both LM and BF muscles of LOW group compared with others remained to be investigated.

Finally, myofiber characteristics in ST muscle were not affected by growth rate in rabbits slaughtered at the same BW. Higher growth rates generally favor both hyperplasia and hypertrophy of myofibers in various species (Hanharan et al., 1973; Ezekwe and Martin, 1975; Rémygnon et al., 1994). The lack of difference in

total fiber number between growth rate groups in the present work might be attributed to the moderate genetic progress obtained for BW relative to experiments in other species. Furthermore, it has been suggested that fiber cross-sectional area or diameter correlates to BW in rabbits (Meister et al., 1974; Reddy et al., 1990; Gondret et al., 2002). The lack of differences in fiber type frequency relative to growth rate confirmed the results of another study carried out on divergently growth-selected chickens (Rémignon et al., 1994); however, higher Type I and lower Type IIB frequencies have been observed in slow-growing compared with fast-growing pigs (Oksbjerg et al., 2000). In raw meat, myofiber content is progressively pushed away from the stress area when meat is aging during the postmortem period, and it is only the connective tissue that is sheared (Lepetit and Culioli, 1994). Therefore, the lowest values for Warner-Bratzler shear force and energies needed to achieve rupture in raw LM from rapid-growing rabbits compared with controls might have resulted from changes in connective tissue rather than in myofiber characteristics. Genetic effects have been evidenced previously for Warner-Bratzler shear forces on cooked LM, but results relative to growth rate variations remain inconclusive (Pla et al., 1998). In contrast, no changes were evidenced for ST texture between the three groups. Differences between muscles in response to growth rate may be attributed to an effect of the dimension of the sample on shear values (Lepetit and Culioli, 1994).

### Implications

Maximizing growth potential by selection is an important goal to ensure an economically viable rabbit industry; however, it has the undesirable effect of increasing adult body weight, leading to less mature animals at the market weight. Interestingly, the findings of the present study did not support the idea that selection for a rapid growth rate had a negative effect on carcass composition and several meat quality indicators. Selection for a lower body weight at a given age provided a model of biological relevance for better understanding of complex genetic variations underlying growth. Although selection for a lower body weight at a given age led to better carcass conformation with more meat relative to bone, and some differences in the meat color, it had limited economic interest because the feed conversion index of the rabbits was degraded.

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