

PANNON BREEDING PROGRAM IN RABBIT AT KAPOSVÁR UNIVERSITY

MATICS ZS.*, NAGY I.*, GERENCSÉR ZS.*, RADNAI I.*, GYOVAI P.*, DONKÓ T.*, DALLE ZOTTE A.†, CURIK, I.‡, SZENDRŐ ZS.*

*Kaposvár University, Kaposvár, H-7400 KAPOSVÁR, Guba S. str. 40, Hungary.

†Department of Animal Medicine, Production and Health, University of Padova, Agripolis, 35020 LEGNARO (PD), Italy.

‡Faculty of Agriculture, University of Zagreb, ZAGREB, Svetosimunska 25, Croatia.

Abstract: In this study, the rabbit breeding programme conducted at the Kaposvár University is extensively discussed. Population history and recorded traits, creation of the different synthetic lines, evolution of their selection criteria, estimation of the genetic parameters and genetic trends are the main elements described. The programme (Pannon rabbit breeding programme) is operated with 1 maternal line and 2 paternal lines. At present the maternal line (Pannon Ka) is selected for number of kits born alive, while the 2 paternal lines are pre-selected for litter weight (Pannon White) and average daily gain (Pannon terminal line), respectively, then they are both selected for thigh muscle volume (based on computer tomography (CT) measurements). All these traits are evaluated by BLUP methodology. According to the genetic parameter estimations, the heritability of the reproductive traits (litter size and litter weight) was low (0.05-0.17 and 0.08-0.17). When the litter size component traits were extended with dominance effects, the magnitude of the dominance components varied between 0.05 and 0.08. Average daily gain and thigh muscle volume were moderately heritable (0.21-0.27 and 0.19-0.25), while heritability estimates of the carcass traits (dressing out percentage and hind part ratio) were high (0.47 and 0.59). Computer tomography based traits showed favourable high genetic correlations with the carcass traits (dressing out percentage: 0.45-0.47 and hind part ratio: 0.59). On the contrary, strong negative correlation was estimated between thigh muscle volume and litter weight (-0.37 and -0.70). The selection responses obtained for all analysed traits were within the range published by the relevant literature. The success of the CT-based selection for improving meat production was justified by different methods (crossing experiment, divergent selection, estimated genetic trends). In addition to the slow increase in the inbreeding level of the Pannon White breed, it also proves the effectiveness of the circular mating scheme used in all three rabbit breeds in the programme.

Key Words: breeding programme, selection response, genetic parameters, divergent selection experiments.

INTRODUCTION

In the selected rabbit lines, the objectives are to improve either reproductive performance for maternal lines or average daily gain (ADG) for sire lines (Baselga, 2004; Garreau *et al.*, 2004; Khalil and Al-Saef, 2008). Generally, the dressing out percentage (DoP) is not included among the selection criteria traits, as this kind of selection requires progeny testing. The disadvantage of the progeny test is that it lengthens the generation interval. In rabbit breeding it was only practised by Varewyck *et al.* (1986) and Szendrő *et al.* (1988). To overcome these difficulties, it is necessary to determine the slaughter value of the animals *in vivo*. Computer tomography (CT) is a technological revolution of *in vivo* non-invasive diagnostics with the representation of cross-sectional imaging that can be used for detailed measurements of different tissues. Organs, anatomical structures and main tissues can be visualized in the CT images, based on the X-ray attenuation differences among body tissues. The CT operated at the Kaposvár University since 1990 offers a unique possibility for carcass trait selection, the greatest advantage of this technology being that evaluation of body composition does not require the use of test slaughters. Thus, self performance tests

Correspondence: I. Nagy, nagy.istvan@ke.hu. Received May 2013 - Accepted September 2014.

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can be used instead of progeny tests. The application of this technique in rabbit breeding is unique worldwide. Over the last 3 decades the researchers at Kaposvár University have developed 3 different rabbit lines, among which 2 lines are selected based on CT measurements. There are 60-65 large rabbit farms in Hungary, producing with about 100000 rabbit does. The 2 slaughter houses process 85-90000 growing rabbits per week. The contribution of the Pannon lines is 44%. Therefore, the Pannon Breeding Programme plays an important role in Hungarian rabbit production, which claims the 4th place in the world when only the rabbit meat trade is concerned. In this review, the main results of our breeding programme are summarised describing the reproductive, growth and slaughter performances of the Pannon White, Pannon Ka and Pannon terminal lines.

POPULATION FOUNDATION AND RECORDED TRAITS

The development of the Pannon White population was initiated at the Kaposvár University at the late 1980s. During the first stage of its development (1988-1990), the population consisted of roughly 100 New Zealand White does selected for ADG and DoP by progeny test. The does were inseminated with the sperm of the bucks located at the Környe rabbit farm. Based on the progeny performances, the ranking of the bucks for ADG and dressing out percentage could be obtained. Involving other small rabbit farms in the process the participating farms could also be ranked. After some years, the progeny test was completed and the development of a new synthetic line –Pannon White– started. This line originated from the New Zealand White and Californian does inseminated with the best bucks from the rabbit farms which participated at the progeny test. After comparing 10 different crossing combinations, the 3 best ones were chosen and served as the basis of the Pannon White rabbit line. Selection targeted the ADG without decreasing the reproductive performance. Among the rabbits with the highest ADG, those with teats numbering 9 or 10 were selected. Selection for the carcass traits based on the CT evaluations also began in 1992 (Szendró *et al.*, 1992a). As the first step, phenotypic correlations were estimated between 36 carcass traits and between the 14 CT-based parameters using 12-13 wk old rabbits weighing 2800 ± 50 g. L-value is measured as the average surface of muscle *longissimus dorsi* between the 2nd and 3rd, and 4th and 5th lumbar vertebrae. Strongest correlations were obtained between the L-value and the DoP ($r=0.53-0.65$) and between L-value and the proportion of the mid-part carcass compared to the reference carcass ($r=0.67-0.71$).

Concerning reproductive traits, teat number can be counted on new born animals in both sexes. This provides very early information on prolificacy. Contrary to the reproductive traits, teat number is a readily heritable trait. Inheritance of teat number among progeny from various mating combinations was studied in 1852 newborn New Zealand White rabbits from 233 matings (Szendró *et al.*, 1991). It was observed that for those progenies whose parents had 10 teats the frequency of large teat numbers (9-11) was much larger compared to those progenies where the parents' teat numbers were only 8. In another paper (Szendró *et al.*, 1992b), the number of teats on parents and progeny was recorded for 4693 New Zealand White rabbits born from 612 matings, and 2336 Californian rabbits born from 284 matings. Effect of teat number of New Zealand White parents on progenies with 10 teats is shown in Figure 1 (Szendró *et al.*, 1992b). This study shows that selection for teat number can be effective.

The selection for teat number was abandoned and the ADG and the L-value became the selection criteria traits. The

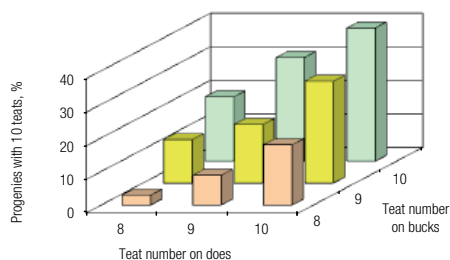


Figure 1: Effect of teat number of the parents on percentage of progenies with 10 teats (based on Szendró *et al.*, 1992b).

first results of our breeding programme were published by Szendró *et al.* (1997). Between 1988 and 1996 an annual response of 1.3-1.4 g/d was obtained for ADG in the population. In addition, registered data for the 10 wk old and adult body weight (BW), litter size and litter weight (at day 21) were also higher at 1996 (Table 1).

The CT-aided selection is accomplished in 2 steps (Szendró *et al.*, 2004). The animals were weighed at 5 and 10 weeks of age, to calculate ADG. The mean ADG of the population ($n=12871$) was 42.1 g/d. Only rabbits showing higher ADG than the average for their kindling batch were selected (based on their individual performance) for the CT measurements. The average ADG of the selected groups was 45.0 g for female and 47.6 g for male rabbits. At

the age of 10.5 wk the rabbits selected for CT scanning are placed in a plastic “container” that serves to restrain 3 rabbits without anaesthesia. Based on 2 CT scans per rabbit, the L-value was measured and expressed in cm². The average L-value of the rabbits selected for breeding animals was higher by 1 and 1.8 cm² in the females and males, compared to that of the rabbits scanned by CT. The second step of CT-aided selection is based on a bivariate BLUP analysis (ADG and L-value) to estimate the breeding values for the L-values. Compared to the total number of growing rabbits with ADG records, 14% of the female and 4% of the male rabbits were selected as breeding animals.

After 2004, L-value was replaced by thigh muscle volume (TMV). TMV is estimated with CT scans taken every 10 mm between the *crista iliaca* of the *os ilium* and the patella. Depending on the dimension/length of the hind legs, 11-12 scans are taken. Voxel frequency of density range belonging to the muscle tissue (between +20 and +200 of the Hounsfield scale) is determined in each scan. Summing these values (of 11-12 scans), the TMV is estimated. Selection is based on BLUP breeding values estimated for TMV. Since 2010 TMV has been replaced by litter weight at day 21. As the growing rabbits do not have reproductive performance, the BLUP values of their parents are used.

Development of the maternal line (M) at the rabbit farm of the Kaposvár University started in 1995 with sperm from some prolific Hungarian and foreign rabbit breeds. The sperm was used to inseminate Pannon White (P) does. In addition to sperm, in 1999 some newborn female and male kits of rabbit breeds showing high reproductive performance were bought. These rabbits were mated within population (and with own rabbits of high prolificacy), forming the base of the maternal line (called Pannon Ka). Since then, the animals are selected in a closed population for number of kits born alive. Pannon Ka was officially recognised as a new synthetic rabbit breed by the Hungarian National Institute of Agricultural Quality Control in 2003.

Formation of the sire line (L) started in 2004 using sperm from some Hungarian and foreign rabbit breeds showing high ADG. The sperm of these rabbit breeds were used to inseminate P does showing high weight gain. The progeny resulting from these inseminations was used to form the foundation of the sire line. As of 2006, animals were selected in a closed population for ADG and TMV (applying CT). The method of selection is the same as described above for these traits in connection with the P line. This line was officially recognised as a new synthetic rabbit breed in 2013.

Summarising the above section, the following rabbit lines are being developed at the Kaposvár University:

P=Pannon White: since its establishment in 1992, this line has been selected for ADG (replaced by 21 d litter weight from 2010) and L-value (replaced by TMV from 2004); adult BW: 4.3-4.8 kg.

M=Pannon Ka (maternal line): since its establishment in 1999, this line has been selected for number of kits born alive; adult BW: 4.0-4.5 kg.

L=Pannon terminal line: since its establishment in 2005 this line has been selected for average daily gain (between the ages of 5 and 10 wk) and for thigh muscle; adult BW: 4.8-5.4 kg

For the 3 lines, genetic evaluations are performed using BLUP methodology.

To control inbreeding rate, each line was divided into 4 groups and these groups have been maintained over time. Females from one group are always mated with males from another group (1♀×4♂; 2♀×1♂; 3♀×2♂; 4♀×3♂) as described in Figure 2. After parturition, the born progeny receive the group number of the sire. The descendents of any buck will be thus be placed back in their group only after 4 generations.

Table 1: Mean performances of the Pannon White rabbit population for growth and reproductive traits (Szendrő *et al.*, 1997).

Trait	Mean	
	1992	1996
Body weight at 10 wk (kg)	2.13	2.31
Litter size	8.04	8.55
Litter weight at day 21 (kg)	2.38	2.56
Individual body weight at day 21 (g)	355	370

After 2004, L-value was replaced by thigh muscle volume (TMV). TMV is estimated with CT scans taken every 10 mm between the *crista iliaca* of the *os ilium* and the patella. Depending on the dimension/length of the hind legs, 11-12 scans are taken. Voxel frequency of density range belonging to the muscle tissue (between +20 and +200 of the Hounsfield scale) is determined in each scan. Summing these values (of 11-12 scans), the TMV is estimated. Selection is based on BLUP breeding values estimated for TMV. Since 2010 TMV has been replaced by litter weight at day 21. As the growing rabbits do not have reproductive performance, the BLUP values of their parents are used.

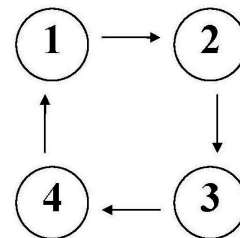


Figure 2: The applied circular mating scheme (the arrows show the direction of the male transfer). (Nagy *et al.*, 2010). 1, 2, 3, 4 are groups within each line.

Table 2: Estimates of heritability for reproductive traits.

Breed	Born total	Born total parity 1-4	Born alive	Born alive parity 1-4	Stillborn	Litter weight parity 1-4
P	0.06-0.10 (a)	0.11-0.19 (b)	0.06-0.09 (a)	0.12-0.17 (b)		0.08-0.16 (e)
P			0.06 (c)			0.10-0.17 (f)
M		0.19-0.31 (b)	0.05 (d)	0.09-0.26 (b)	0.02 (a)	

M: Maternal line; P: Pannon White; parity 1-4: records obtained at the first 4 parities are considered as separate traits; (a) Nagy *et al.* (2013a); (b) Nagy *et al.* (2011c); (c) Garreau *et al.* (2000); (d) Gyovai *et al.* (2009); (e) Nagy *et al.* (2011b); (f) Gyovai *et al.* (2012).

GENETIC ANALYSES

Additive genetic components

Heritability estimates of reproduction traits are summarised in Table 2. Depending on the purposes of the different studies, the repeated parturitions of the same rabbit does were evaluated using either repeatability (Garreau *et al.*, 2000; Gyovai *et al.*, 2009; Nagy *et al.*, 2013) or multi-trait (Gyovai *et al.*, 2012; Nagy *et al.*, 2011b, 2011c) animal models. Heritability estimates for the litter trait components (number of kits born alive, dead and total) were generally low (less than 0.20), but it can be noted that lower heritability estimates were obtained in the P line compared to the M line. This finding may be connected to the longer selection history of the former line, so perhaps it is more homogeneous compared to the M line. When the estimates were made using the whole dataset, higher values were estimated compared to the heritabilities of the successive parities treating them as separate traits. The highest values were observed for the 3rd parity (Nagy *et al.*, 2011c). Other authors (Rastogi *et al.*, 2000; García and Baselga, 2002a, 2002b; Piles *et al.*, 2006; Mantovani *et al.*, 2008) reported similar heritability estimates for the total number of kits born as reported by our studies (Table 2). Heritability of the litter weight at day 21 was moderately low, varying between 0.08 and 0.17 depending on the parity. Similar values were reported by other authors (Ayyat *et al.*, 1995; Lukefahr and Hamilton, 1997; Rastogi *et al.*, 2000; Moura *et al.*, 2001).

Heritability estimates of the growth, carcass and CT related traits are provided in Table 3. The estimated values of the BW at 10 wk of age and those of the ADG were moderate (0.20-0.30) and similar to the estimates of Lukefahr *et al.* (1996), Gómez *et al.* (1998) and García and Baselga (2002c). On the contrary, higher heritabilities were estimated by Moura *et al.* (1997). The different heritability estimates may be connected to the different ages of the populations analysed by the different authors. Dressing out percentage showed high heritability (0.47-0.48). These estimates were very similar to the reported values of Lukefahr *et al.* (1996) and Värewyck *et al.* (1986) but different of those of Ferraz *et al.* (1992a) Lukefahr *et al.* (1992, 1993) Krogmeier *et al.* (1994), who reported lower heritability values. The heritability estimate of the hind part ratio was high (0.59) and for this trait there was no available literature to compare our results. The L-value had moderate heritability (0.33) compared to DoP, but this value is much higher than that of the TMV (0.19-0.25).

Table 3: Estimates of heritability for production, carcass and computer tomography measured traits.

Breed	ADG	BW10	DoP	L-value	TMV	HPP
P	0.25 (a)	0.20 (a)	0.47-0.48 (c)	0.33 (c)	0.21 (d)	0.59 (e)
P	0.27 (b)	0.26 (b)			0.19 (e)	
P	0.24-0.25 (c)				0.20 (g)	
P	0.27 (d)					
P	0.30 (e)					
P	0.28 (f)					
P	0.21 (g)					
L	0.23 (h)				0.25 (h)	

L: terminal line; P: Pannon White; ADG: average daily gain between the ages of 5 and 10 wk; BW10: body weight at 10 wk of age; DoP dressing out percentage; HPP hind part percentage; L-value: average surface of muscle *longissimus dorsi* between the 2nd and 3rd, and 4th and 5th lumbar vertebrae; TMV: thigh muscle volume; (a) Garreau *et al.* (2000); (b) Nagy *et al.* (2006a); (c) Nagy *et al.* (2006b); (d) Gyovai *et al.* (2008); (e) Nagy *et al.* (2010b); (f) Nagy *et al.* (2011a); (g) Gyovai *et al.* (2012); (h) Nagy *et al.* (2013b).

Dominance components

Nagy *et al.* (2013a) estimated the genetic parameters of litter size components of the P rabbits, extending the repeatability animal models with dominance effects. The magnitude of the dominance components were 0.05, 0.05 and 0.08 for the number of kits born alive, stillborn and born total, respectively. When the dominance components were included in the models, the additive genetic effects, but especially the permanent environmental effects, decreased. Thus, a partial confounding was observed between the dominance and permanent environmental components. In the optimal situation, inclusion of the dominance component should only decrease the residual components, leaving the other variance components unchanged. Sánchez *et al.* (2005) reported a similar tendency to the results of our study for the longevity of does, although in their case the authors noted that their dominance estimates were influenced by statistical uncertainty and non-optimal data structure. In contrast, Fernández *et al.* (2010) estimated negligible dominance component for litter size at weaning (0.017).

Genetic correlation

In the P and M lines, for number of kits born total or alive, the genetic correlation coefficients between the number of the successive parities were high (>0.56). The lowest genetic correlations were estimated between the 1st and 4th parities (0.64 and 0.56 for the number of kits born total and alive, respectively). The strongest correlations were obtained between the 3rd and 4th parities (0.93 and 0.96 for the same traits) (Nagy *et al.*, 2011c). The interpretation of this finding is that the litter size after the 1st and 2nd parturition (when the rabbits did not reach their maximum performance) can be considered as a separate trait compared to the litter size of the latter parities. Piles *et al.* (2006) reported the results of a similar study. The number of kits born in total and alive of the successive parities showed high genetic correlation coefficients in one of the examined lines (>0.80) (called line A), but wider ranges of genetic correlation coefficients were obtained in the other lines (called Prat and V) (0.53-0.84 and 0.39-0.83 for the number of kits born total and alive, respectively). The successive 21 d litter weights showed moderately high to high genetic correlations (0.47-0.89). The values obtained were similar to those achieved for litter size components. The estimated genetic correlation coefficients for other traits are presented in Table 4. The genetic correlations that we estimated between the ADG and BW at 10 wk of age and litter size were low (0.06-0.18) and coincided with the reported values of Gómez *et al.* (1998). Contrary to these studies, Rochambeau *et al.* (1989) estimated negative values. Camacho and Baselga (1990) reported favourable genetic correlation coefficients in 2 sire lines selected for growth, but opposite results were found in maternal lines selected for litter size. These authors suggested that the results could be connected to maternal effects. According to their evaluations, the litter size at day 21 and the ADG showed moderately low genetic correlation (0.11-0.36). Similar genetic correlation estimates were reported between litter size at weaning and ADG (0.13-0.20). Using the same traits, Gómez *et al.* (1998) estimated negative genetic correlation coefficients (-0.16). Nevertheless, it has to be noted that

Table 4: Genetic correlation estimates between the examined traits.

	ADG	BW10	TMV	L-value
NBA	0.06-0.18 (a)	0.07-0.09 (a)		
LW21 parity 1-4	0.11-0.36 (b)		-0.37-0.70 (b)	
BW5	-0.19 (c)	0.54 (c)		
BW10	0.72-0.74 (a)			
	0.76 (c)			
TMV	0.14 (e)			
	0.06 (f)			
DoP	-0.32 (d)			0.47 (d)
L-value	-0.21 (d)			
HPP	-0.08 (f)		0.59 (g)	

ADG: average daily gain between the ages of 5 and 10 wk; BW5: body weight at 5 wk of age; BW10: body weight at 10 wk of age; NBA: number of born alive; DoP: dressing out percentage; HPP: hind part percentage; L-value: average surface of muscle *longissimus dorsi* between the 2nd and 3rd, and 4th and 5th lumbar vertebrae; LW21 parity 1-4: 21 d litter weight at parities 1-4; TMV: thigh muscle volume; (a) Garreau *et al.* (2000); (b) Gyovai *et al.* (2012); (c) Nagy *et al.* (2006a); (d) Nagy *et al.* (2006b); (e) Gyovai *et al.* (2008); (f) Nagy *et al.* (2010b); (g) Nagy *et al.* (2010c).

the magnitude of the genetic correlation between the growth and reproductive trait was generally low, which suggest that the direction (positive or negative) of the estimates has limited importance.

Gyovai *et al.* (2012) reported an unfavourable genetic correlation between the litter weight at day 21 and TMV. The estimated correlation coefficient was moderate for the 1st and 2nd parities (−0.37 for both), but high for the 3rd and 4th parities (−0.53 and −0.70). Compared to other rabbit breeds, Szendrő *et al.* (2010) observed that P rabbits have a lower amount of perirenal fat, which may suggest that the CT-aided selection decreased the rabbits' fat depots. This finding is unfavourable and can affect the P does, as it is known that energy deficit and depletion of body stores lead to a decrease in reproductive performance (Fortun-Lamothe, 2006). Based on this result, the selection criteria of the P breed was changed from the ADG to the litter weight at day 21. Estimated genetic correlations between ADG and DoP, L-value or hind part ratio were negative and moderate or low (−0.32 −0.21 and −0.08, respectively). The ADG showed a positive but low genetic correlation with the TMV (0.06-0.14, Table 3). The negative genetic correlation is unfavourable to selection on ADG and DoP. However, since 2004 the TMV has been measured and this trait is positively correlated with ADG. Relatively high genetic correlation was reported between the L-value and DoP (0.47). This result is very important, as it proves the efficiency of the CT-aided selection. A favourable genetic correlation (0.59) was obtained between the TMV and hind part ratio. Based on this last finding, the CT-aided selection is efficient in increasing the quantity of the hind leg meat.

Genetic trends

The estimated annual genetic trends are summarised in Table 5. In the P breed we observed negligible genetic trends for number of kits born alive (0.01), but this finding can be explained by the fact that this line was not selected for litter size. Moura *et al.* (2001) and Santacreu *et al.* (2005) reported similar values (0.03-0.05 kit/yr), Garreau *et al.* (2005), García and Baselga (2002a, 2002b) and Lenoir and Garreau (2009) obtained much larger genetic trends (0.12 kit/yr). In the M line, after 10 yr the litter size will only increase by 0.3-0.4 kits. Still this trend is substantially larger compared to the P line and this tendency remained the same when the estimated trends were given in additive genetic standard deviation units (0.054 vs. 0.016, respectively). The low genetic trends can partly be explained by the low heritability of the selection criterion.

For ADG, the estimated genetic trends were 0.6-1.0 g/yr and 1.5 g/yr for the P and L lines, respectively. According to our estimates, BW at 10 wk of the P line increases 18 g/yr. In the P line, the annual genetic trend of ADG was lower during the first 5 yr of selection (until 2008) than afterwards. The genetic trend of the L line for the same trait was higher than that of the P line. Expressing the genetic trend in additive genetic standard deviation units, the estimated trend for ADG for P and L lines became similar (0.701 and 0.739, respectively). Other authors reported similar annual genetic trends (0.45-1.23 g/d) (Estany *et al.*, 1992; Moura *et al.*, 1997; Piles and Blasco, 2003) for this trait.

Similarly to ADG, the estimated genetic trends for the TMV was higher in the L (5.8 cm³) than in the P line (4.0 cm³). This finding may be the consequence of the higher TMV heritability of the L line compared to P rabbits. When the genetic trend was converted to additive genetic standard deviation units for the L and P lines, then the magnitude of the differences decreased (0.338 vs. 0.307, respectively).

Table 5: Selection response (estimated annual genetic gain per year) in different traits.

Traits	Breed	Gain/yr	References
No. of kits born total	P	0.008	Nagy <i>et al.</i> (2011c)
No. of kits born total	M	0.03	Nagy <i>et al.</i> (2011c)
No. of kits born alive	P	0.01	Nagy <i>et al.</i> (2011c)
No. of kits born alive	M	0.04	Gyovai <i>et al.</i> (2009)
No. of kits born alive	M	0.03	Nagy <i>et al.</i> (2011c)
Average daily gain (g/d)	P	0.64	Garreau <i>et al.</i> (2000)
Average daily gain (g/d)	P	1.05	Gyovai <i>et al.</i> (2008)
Average daily gain (g/d)	L	1.49	Nagy <i>et al.</i> (2013)
Body weight at 10 wk (g)	P	18.5	Garreau <i>et al.</i> (2000)
Thigh muscle volume (cm ³)	P	4.01	Gyovai <i>et al.</i> (2008)
Thigh muscle volume (cm ³)	L	5.84	Nagy <i>et al.</i> (2013)

L: terminal line; M: Maternal line; P: Pannon White.

Table 6: Effect of divergent selection for L-value on carcass traits (only the males were selected) (Szendrő *et al.*, 1996).

Traits	Min sel	PlusPlus sel	P-value
L-value (cm ²)	19.6	20.8	0.05
Dressing out percentage (%)	62.3	64.1	0.05
Fore part of carcass (g)	397	395	NS
Mid part of carcass (g)	430	452	0.05
Hind part of carcass (g)	513	527	0.05
Skin weight (g)	386	370	0.05
Gastrointestinal tract weight (g)	379	356	0.05

Min sel: the 5 male rabbits with the lowest L-value.

PlusPlus sel: the 5 male rabbits with the highest L-value at the second generation.

Divergent selection experiments

A divergent selection experiment was carried out to determine the effect of selection for L-value (Szendrő *et al.*, 1996) based on the individual performances (mass selection). With the help of CT scanning, the best 5 (Plus sel) and the worst 5 male rabbits (Min sel) were selected on the basis of L-value at the age of 10 wk. Thereafter, randomly chosen does were inseminated with the semen of these bucks. In the 2nd step, the 5 best males (PlusPlus sel) were chosen from the progenies of Plus bucks. Table 6 shows the carcass traits of Min and PlusPlus bucks which were born on the same day and slaughtered at the same weight (2784 g). It can be seen that the CT-based selection improved the dressing out percentage by 1.8%, increased the weight of mid and hind part of carcass (5.1 and 2.7%, respectively), and decreased the weight of skin and gastrointestinal tract (4.1 and 6.1%, respectively). It may be concluded that the selection on L-value is an effective method to improve the carcass traits of rabbits, while the skin and gastrointestinal tract ratios decrease as a side effect.

The effects of selection for TMV on the production and slaughter performance of growing rabbits were tested by divergent selection experiment (Szendrő *et al.*, 2012a). Pannon White rabbits were selected to increase (Plus selected) or decrease (Min selected) their TMV over 2 generations. Production and slaughter traits of their offspring (the 3rd generation) were measured (Table 7). Selection had no effect on ADG and BW at 10 wk of age. Plus selected rabbits had lower feed intake (FI) and better feed conversion ratio (FCR) and larger (TMV) compared to the Min selected group. The ratio of the full gastrointestinal tract compared to BW was lower for the Plus selected rabbits but the differences were not significant. Compared to the reference carcass, the hind part ratios were higher and the perirenal fat (PFaP) was lower in the Plus selected group. It was thus shown that CT-aided selection can efficiently increase the TMV. At the same time, the volume of fat depots decreased while FCR also improved. Results of the experiment provide some evidence for effectiveness of CT based selection. If the selection objective is to increase the TMV, not only the carcass traits but also the FI and FCR will improve.

Analyses related to inbreeding

Analysing the pedigree of the P breed, Nagy *et al.* (2010a) reported the longest generation interval (1.4 yr) for the buck-son path. The reason for these results is that the productive period of the does is short due to their intensive replacement (110% yr). Similar tendencies were observed by Planinc *et al.* (2012). The pedigree completeness of the breeding rabbits born in 2007 was above 90% up to the 9th generation, resulting in a high complete generation equivalent of these animals. The average inbreeding coefficient gradually increased (Figure 3) and the largest increase was observed between 2005 and 2006 (1.29%). On the contrary, over the last 4 yr analysed the average relatedness was stable (Figure 3). The ten and thirty most contributing founders accounted for 42% and 73% of the total inbreeding, respectively. The effective population size (Figure 4) of the reference population 2007 varied between 37 and 91 depending on the applied method (inbreeding effective population size vs. realised effective population size). During the first few years (1993-1995), as shown in Figure 5, a drastic reduction was found for the effective numbers of founders (the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study) and ancestors (the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of a population). Except for the effective numbers of founder genome equivalents (the number of founders that would be expected to produce the same genetic diversity

Table 7: Effect of divergent selection for volume of thigh muscle on productive performance and carcass traits in the third generation (Szendrő *et al.*, 2012).

Traits	Minus selected	Plus selected	Sig.
Thigh Muscle Volume (cm ³)	309	336	0.018
Feed intake (5-10 wk) (g/d)	138	128	0.002
Average daily gain (5-10 wk), g/d	44.7	45.7	0.461
Body weight (BW) at 10 wk (kg)	2471	2474	0.757
Feed conversion rate	3.01	2.81	<0.001
Ratio of the full gastrointestinal tract compared to BW (%)	18.1	16.7	0.415
Dressing out percentage (%)	60.4	61.5	0.396
Fore part to reference carcass (%)	30.1	29.4	0.066
Mid part to reference carcass (%)	30.3	30.0	0.335
Hind part to reference carcass (%)	36.3	38.2	0.015
Perirenal fat to reference carcass (%)	2.40	1.90	0.005

as in the population under study if the founders were equally represented and no loss of alleles occurred), the values of all other parameters decreased by 50% between 1993 and 1995. Some years later (in 2008, 2009), the average inbreeding level of the population was 6.3% and this value was much lower than those observed by Kerdiles and Rochambeau (2002) in French rabbit strains 2066 (27%) and 1077 (22%). The P line had a complete generation equivalent of 12.1 (Nagy *et al.*, 2011b). This latter number is exceptionally large and can only be compared to some horse pedigrees (Curik *et al.*, 2003). A similar value (11.0) was reported by Planinc *et al.* (2012) for Sika rabbits. The applied circular mating system (see in Material and Methods) was effective concerning the inbreeding rate and loss of genetic diversity of the P population. Results justify the importance of continuous monitoring to detect genetic load and loss of genetic diversity.

Examining the effect of inbreeding on the rabbits' reproductive performances, Nagy *et al.* (2012) reported a significant decrease in total number of kits born (-0.34) and number of kits born alive (-0.45) per 10% increase of inbreeding coefficient of the litters'. The same increase of the does' inbreeding coefficients increased the number of stillborn by 0.18 kits. Contrary to these results, Moura *et al.* (2000) found that number of kits born alive was not affected by litter inbreeding, while a 10% increase in the does' inbreeding coefficient reduced this trait by 0.81 kits. Ragab and Baselga (2010) grouped the inbreeding coefficients to several classes and treated inbreeding depression as class effect. They also reported harmful effects of inbreeding for the number of kits born alive in several lines that

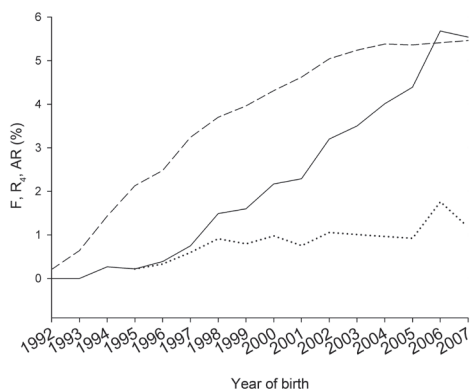


Figure 3: Trends for the mean inbreeding related to total (F) (—) and four (.....) generation (F₄) pedigree, and the average of relatedness (AR) (- - -) for Pannon white rabbits. (Nagy *et al.*, 2010).

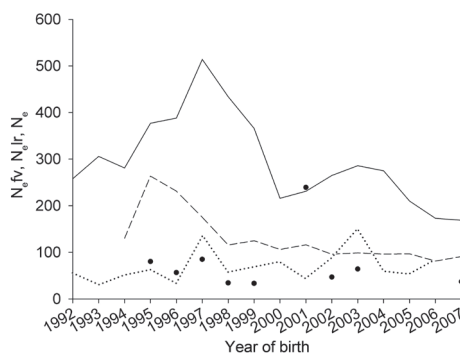


Figure 4: Trends in the number of breeding rabbits (—), family variance effective population size (.....), inbreeding effective population size (• •) and realized effective population size (- - -) for Pannon white rabbits. (Nagy *et al.*, 2010).

had similar inbreeding levels to the population analysed by Nagy *et al* (2012).

The 10% increase of the rabbit does' inbreeding coefficient coincided with the 0.028 kg decrease of the 21 d litter weight, but this result was not significant (Nagy *et al.* 2011b). This result is surprising, as the inbreeding depression is mostly pronounced in traits related to fitness (Curik *et al.*, 2003). Moura *et al.* (2000) reported an inbreeding depression of 0.21 kg of the litter weight per 10% increase of the does' inbreeding coefficient. The estimated inbreeding depression for litter weight (per 10% increase of inbreeding coefficient) was 0.57 g for the L line (Nagy *et al.*, 2013), but no inbreeding depression was observed for TMV. Using the same scale, Ferraz *et al.* (1992b) reported inbreeding depression between 5 and 130 g for BW measured at 5 and 10 wk of age. Related to inbreeding, it can be concluded that despite its long history and closed population structure, the Pannon White population's inbreeding level is relatively low and no severe inbreeding depression can be expected in the near future.

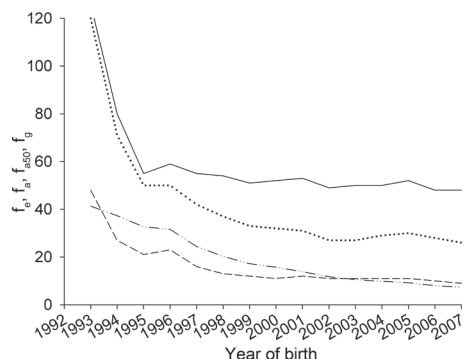


Figure 5: Trends in the probability of gene origin; effective number of founders (f_e —), effective number of ancestors (f_a), number of ancestors explaining the 50% genetic variability (f_{50} —) and effective number of founder genomes (f_g —) for Pannon white rabbits. (Nagy *et al.*, 2010).

Crossing experiments

In the experiment of Metzger *et al.* (2006a) the ADG, carcass traits and meat quality of Hyplus hybrid (HH, offspring of Hyplus PS59 bucks and Hyplus PS19 does), purebred P rabbits (PP, offspring of P bucks and P does) and their crossbreds (PH: offspring of P bucks and H does; HP: offspring of H bucks and P does) were compared. P rabbits were selected for ADG and L-value, while H females and H males were selected on prolificacy and ADG, respectively. Rabbits of HP genotype had the highest ADG, while those of PP genotype had the lowest (38.9 and 36.6 g/d, respectively). P breed had an advantageous influence on DoP (Table 8) and on the weight of the *longissimus dorsi* muscle (Table 8). The fat content of the carcass was lower in the offspring of the H bucks (Table 8). Significant differences were found between the meat samples of progenies of purebred P and the H terminal cross rabbits in the moisture and fat content of hindleg meat (moisture content: PP: 75.5% and HH: 76.1%; $P < 0.05$; fat content: PP: 2.38% and HH: 1.46%).

In these tests, the carcass traits of rabbits were compared when the same maternal stocks were mated with bucks of 2 well-known hybrids selected for growth traits or with P bucks (Metzger *et al.*, 2006b). Three experiments were carried out at the same time. Experiment 1: P or H males were crossed with P does (PP and HP). Experiment 2: P, H or Zika terminal (Z) bucks were crossed with H parent does (PH, HH and ZH). Experiment 3: P or Z males were crossed with a Maternal line (M) stock (PM and ZM). In all the experiments, hybrid males increased their BW. Results are presented in Table 9. Mating the same maternal stock with H or P bucks, the BW at slaughter of the offspring of H males was higher than that of the offspring of P bucks. The most important carcass traits differences were found in rabbits originated from P males. Genetic origin influenced the DoP, which was 0.5% higher in PP rabbits compared to

Table 8: Comparison of slaughter performance of purebred and crossbred rabbits (based on Metzger *et al.*, 2006a).

Traits	Genotype			
	PP	PH	HP	HH
Dressing out percentage (%)	58	58.7	57.7	57.6
Weight of the muscle <i>longissimus dorsi</i> (g)	152	143	137	136
Fat content of the carcass (%)	1.15	1.16	0.89	0.85

PP: offspring of Pannon White bucks and Pannon White does; PH: offspring of Pannon White bucks and Hyplus hybrid does; HP: offspring of Hyplus hybrid bucks and Pannon White does; HH: offspring of Hyplus hybrid bucks and Hyplus hybrid does.

Table 9: Comparison of slaughter performance of purebred and crossbred rabbits (based on Metzger *et al.*, 2006b).

Traits	Genotype		
	Experiment 1	PP	HP
Body weight at slaughter (g)	2644	2758	
Dressing out percentage (%)	60.6	60.1	
Longissimus dorsi, compared to the reference carcass (%)	11.5	11.6	
Experiment 2	PH	HH	ZH
Body weight at slaughter (g)	2611	2671	2890
Dressing out percentage (%)	59.6	59.7	58.7
Longissimus dorsi, compared to the reference carcass (%)	11.2	10.8	
Experiment 3	PM	ZM	
Body weight at slaughter (g)	2534	2677	
Dressing out percentage (%)	61.0	59.5	
Longissimus dorsi, compared to the reference carcass (%)	11.5	10.6	

PP: offspring of Pannon White bucks and Pannon White does; HP: offspring of Hycole terminal bucks and Pannon White does; PH: offspring of Pannon White bucks and Hycole parent does; ZH: offspring of Zika terminal bucks and Hycole parent does; PM: offspring of Pannon White bucks and Maternal line does; ZM: offspring of Zika terminal bucks and Maternal line does.

the HP group in Experiment 1, 1% higher in PH and ZH genotypes compared to HH animals in Experiment 2, and 1.5% higher in PM than in ZM rabbits in Experiment 3. The ratio of the MLD to reference carcass weight was also higher in rabbits derived from P males in Experiments 2 and 3, while it did not differ in Experiment 1 (Table 9).

The effect of dam and sire genotypes on productive and carcass traits was also examined (Szendró *et al.*, 2010). P and M does were inseminated with the sperm of P, M, L or H bucks. The mature body size of the M and P genotypes was medium, and that of the L and H genotypes was large. Only P and L rabbits were selected for carcass traits based on CT scanning data. Data of the main production and carcass traits are summarised in Table 10. ADG (5.7%) and FCR (6.2%) of the progeny of P does were better than those of the progeny of the M does. The weight of the chilled carcass and body parts was greater for the progeny of the P does. DoP did not differ, but the ratio of the hind part compared with the reference carcass was greater in the P group; however, the ratio of the fore part was greater in the M group. Examining the effect of the genotype of the sires, the BW and ADG were greater in groups H and L, whereas the progeny of M sires were inferior. Order of BW at 11 wk of age as follows: H>L>P>M. Similar differences were found for ADG and FI. The weights of the chilled carcass and of the body parts were the greatest for the progeny of the H sires, and the smallest in the M group. The differences between the DoP of the groups were not significant.

Table 10: Effect of the dam's and sire's genotypes on the productive performance of growing rabbits (Szendró *et al.*, 2010).

Trait	Age (wk)	Genotype of does		Genotypes of bucks				Effect of genotypes	
		M	P	M	P	L	H	Does	Bucks
Body weight (g)	11-	2.696	2.747	2.585 ^a	2.678 ^{ab}	2.793 ^{bc}	2.918 ^c	0.074	<0.001
Average daily gain (g/d)	5-11	42.4	44.8	41.2 ^a	42.9 ^{ab}	44.8 ^b	47.6 ^c	<0.001	<0.001
Feed intake (g/d)	5-11	127	127	118 ^a	125 ^{ab}	129 ^{bc}	135 ^c	0.865	<0.001
Feed conversion Ratio	5-11	3.00	2.83	2.86 ^{ab}	2.91 ^{ab}	2.88 ^{ab}	2.84 ^b	<0.001	0.019
Dressing out Percentage (% HCW)		60.3	60.7	60.5	60.8	60.7	60.0	0.069	0.271
Fore part (% RCW)		26.5	26.2	26.1 ^{ab}	26.0 ^a	26.5 ^{bc}	26.4 ^{abc}	0.025	<0.001
Mid part (% RCW)		34.3	34.2	34.4	34.2	34.2	34.1	0.409	0.330
Hind part (% RCW)		37.2	37.7	37.4 ^{ab}	38.0 ^c	37.2 ^{ab}	37.5 ^{bc}	<0.001	<0.001
Perirenal fat (% RCW)		2.01	1.87	2.00	1.79	2.06	1.94	0.113	0.178

M: Maternal line; P: Pannon White; L: Terminal line; H: Terminal line of Hycole. HCW: hot carcass weight; RCW: reference carcass weight.

^{a,b,c} within a row (for the effect of sires' genotype), means without a common superscript letter differ ($P < 0.05$).

Table 11: Productive, carcass and meat quality traits of Pannon Ka, Pannon White and Pannon Large growing rabbits (Szendró *et al.*, 2009a,b; Dalle Zotte *et al.*, 2009).

Traits	M	P	L	Sig.
Average daily gain (g/d)	44.6	46.2	54.6	<0.001
Body weight at 11 wk (g)	2458	2667	2949	<0.001
Feed conversion ratio	2.95	2.81	2.93	0.257
Dressing out percentage (% HCW)	60.2 ^a	61.3 ^b	61.1 ^b	0.031
Fore part (%RCW)	26.0 ^b	25.7 ^a	26.9 ^b	<0.001
Mid part (% RCW)	34.5	34.2	33.9	0.111
Hind part (% RCW)	37.3 ^a	38.2 ^b	37.2 ^a	<0.001
Polyunsaturated fatty acid content	24.9 ^a	31.9 ^b	27.8 ^{ab}	0.022
Omega-3	2.00	2.54	2.23	0.92

L: terminal line; M: Maternal line; P: Pannon White. HCW: hot carcass weight; RCW: reference carcass weight.

^{a, b, c} within a row means without a common superscript letter differ at $P < 0.05$.

The ratio of the fore part was greater in groups L and H, but the ratio of the middle part was not different. The ratio of hind part related to the reference carcass was largest in progeny of P and least in L group. It was concluded that the production of growing rabbits was affected by the adult BW of their sires, whereas the carcass traits were influenced by their own adult BW and by the CT-based selection.

Gross profit was calculated by Szendró *et al.* (2012b) on the level of production chain (including farm and slaughterhouse). Calculating on equal slaughter weight of 2.5 kg, the highest gross profit was found in P, followed by PL. The best cost to revenue ratios and gross profit to cost ratios were found in the case of PL and P, respectively. Despite the general negative correlation between adult weight and carcass traits, on average, the performance of progenies of P does and the progenies of L males were superior. Comparing the pure genotypes, P rabbits reached the best results, followed by the L breed and the M one. In general, long-term CT-based selection on carcass traits leads to the development of more valuable animals in terms of cost to revenue, gross profit to cost ratios and efficiency.

The main productive, carcass and meat quality traits of 3 genotypes are summarised in Table 11. It can be concluded that production traits were mainly affected by the adult weight of the genotypes: the order among the breeds in BW, ADG and FI were: M<P<L. The FCR and mortality were similar (Szendró *et al.*, 2009a). The DoP of the P rabbits exceeded that of the M group, but L rabbits also showed favourable results (Szendró *et al.*, 2009b). This can be explained by selecting the P and L rabbits (for 14 and 3 yr, respectively,) for their L-value (between 1993 and 2004, Nagy *et al.*, 2006b; Szendró *et al.*, 2004) and their TMV (since 2004; Szendró *et al.*, 2008). The ratio of hind part was highest for P rabbits, and that of the fore part in L rabbits. No significant differences were found in mid part. The differences between the carcass part ratios for L and P rabbits can be explained by the different duration of the CT-based selection. It can be concluded that contrarily to the data provided in literature, although slaughter performances were unaffected by the adult weight of the genotypes, the effect of CT-based selection was evident in rabbits of different genotypes slaughtered at the same age.

Our study revealed that long-term CT-based selection is effective in increasing meat leanness and polyunsaturated fatty acid content. Certain other meat quality variables appear to be affected to lesser extent (Dalle Zotte *et al.*, 2009).

CONCLUSIONS

Because the heritability estimates of the litter size components are low and the estimated genetic trends are small, substantial improvement of these traits can only be expected on the longer term. For ADG, both the estimated heritabilities and the estimated genetic trends were matched with the main results from the literature. The CT-based traits showed lower heritabilities compared to those of the DoP and hind part ratio. This finding calls our attention to improving the efficiency of CT scanning. However, the selection conducted for L-value and TMV were still efficient, as these traits had favourable genetic correlations with important carcass traits. Because of the CT-aided selection applied, it can be presumed that the litter weight at day 21 decreased as a side effect due to the decreased fat depots. This unfavourable process was stopped by changing the selection criteria, including the litter weight at day 21. The

CT-aided selection proved to be successful, as shown by the estimated genetic parameters and the genetic trends in the divergent selection experiments and the crossing experiments. Based on economic calculations, the CT-aided selection generates a substantial profit at slaughterhouse level.

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