Genetic diversity and population structure of the synthetic Pannon White rabbit revealed by pedigree analyses[1]

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ABSTRACT: Demographic history, current status, and efficiency of the mating strategy were analyzed using the pedigree of Pannon White (PW) rabbits born between 1992 and 2007. Potential accumulation of detrimental effects and loss of genetic diversity were also considered. Calculations and estimates were done most often for rabbits born in 2007, whereas other reference populations (REFPOPXXXX) were specified explicitly. The pedigree contained 4,749 individuals and 580 founders, and its completeness was 82.1% up to 10 and 94.5% up to 5 generations, respectively. Generation intervals through different pathways averaged 1.2 yr. When adjusted to the pedigree completeness, the amount of inbreeding (F_i) of rabbits was comparable (5.54%) with that of other livestock populations, whereas the 10 (30) founders contributing the most to inbreeding explained a large part of the population inbreeding [i.e., 42.24% (73.18%)]. The ancestral inbreeding coefficient of REFPOP2004 (10.67%) was one-half that of REFPOP2007 (20.66%), showing its strong dependence on pedigree length. Family variance, inbreeding, and realized effective population size were 84.18 (REFPOP2006; this variable could not be calculated for the last year examined), 37.19, and 91.08, respectively. The effective numbers of ancestors, founders, and founder genomes were 48, 26, and 7.33, respectively. Although the circular mating scheme applied was generally effective, the large accumulated reduction in genetic variability indicates the need to revise and improve the current breeding strategy.

Key words: genetic diversity, inbreeding coefficient, Pannon White rabbit, pedigree analysis

INTRODUCTION

Rabbit meat production is approximately 1.1 million metric tons worldwide. China, Italy, Spain, and France are the greatest producers (FAOSTAT, 2008). Being the ninth largest producer and, after China, the second exporting country of rabbit meat, Hungary has a special place in world rabbit production (Szendrő and Szendrő, 2008). Domestic consumption is negligible and the rabbit meat produced in Hungary is mainly exported to Italy, Switzerland, and Germany, usually as whole carcasses. The rest of the export consists of dissected and processed products (Kling, 2007). The Pannon White (**PW**) rabbit breed, developed and selected at Kaposvár University, has a large impact on the Hungarian rabbit breeding sector because 43% of the national rabbit breeding stock was PW in 2004 and 20% was PW in 2007.

In domestic animals, pedigree analysis is a valuable tool for quantifying detrimental genetic effects (Ballou, 1997; Gulisija and Crow, 2007; Man et al., 2007) and loss of genetic variation (Boichard et al., 1997; Sölkner et al., 1998). A large number of studies in horses (Zechner et al., 2002; Cervantes et al., 2008b) and cattle (Sölkner et al., 1998; Gutiérrez et al., 2003) have been based on pedigree analyses. Although pedigrees are often recorded in rabbit breeding, only Kerdiles and de Rochambeau (2002) have implemented them as a tool in the analysis of 2 French rabbit strains.

The main objective of this study was to analyze the demographic history, current status, and efficiency of

Table 1. Number of Pannon White breeding animals born in successive years

Year of birth	Does	Bucks
1992	201	57
1993	265	41
1994	223	58
1995	326	51
1996	350	38
1997	439	75
1998	403	31
1999	292	74
2000	158	58
2001	164	67
2002	211	54
2003	235	51
2004	224	51
2005	160	50
2006	112	61
2007	105	64

the mating strategy for PW rabbits with respect to potential accumulation of detrimental effects and loss of genetic diversity through pedigree data. The results obtained will complement production variables and provide the basis for a long-term breeding strategy for the breed.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because analyses were carried out on existing data attained under standard farm management. The records analyzed were controlled by the head of the experimental farm of Kaposvár University between 1992 and 2007.

Population Foundation and Management

The development of the PW population was initiated at Kaposvár University in the late 1980s. During the first stage of its development (1988 to 1990), the population consisted of roughly 100 New Zealand White does selected for ADG and dressing percentage by progeny testing. During the second stage, in 1991, New Zealand White rabbits were reciprocally crossed with Californian rabbits (and New Zealand-type rabbits of various origins). The progeny of the crosses showing the best BW gain and dressing percentage served as the basis for the PW rabbits, a new synthetic population. The third stage of the program (begun in 1992) involves a mass selection for ADG and carcass traits (applying computer tomography), using a closed herd book. The generations were overlapping. A detailed description of the foundation of the PW is given in Nagy et al. (2006), and demographic variables are given in Table 1.

To avoid mating of close relatives and increased inbreeding, a circular mating system was used, in which the population was divided into 4 groups. The matings among the groups have been carried out in the follow-

ing way: group 1 female × group 4 male; group 2 female × group 1 male; group 3 female × group 2 male; group 4 female × group 3 male (Figure 1). After the matings, the progeny born receive the group number of the sire.

Generation Interval and Pedigree Information

Generation Interval. The generation interval was calculated as the average age of parents at the birth of the progeny kept for the reproduction (Gutiérrez and Goyache, 2005). This was computed for all 4 parent-progeny pathways.

Pedigree Information. The analysis was based on the pedigree of breeding rabbits born from January 1, 1992, to December 31, 2007. The pedigree contained 4,749 different individuals. Ancestors with 2 unknown parents (n = 363) were considered founders. For ancestors with only 1 known parent (n = 218), the unknown parent of the new pedigree members was proclaimed as a founder (Lacy, 1989). Thus, the pedigree was extended to 4,967 animals. For each offspring, pedigree completeness was assessed by computing the proportion of its known ancestors per generation (MacCluer et al., 1983). The number of equivalent generations known in the pedigree was computed as the sum of $(1/2)^n$, where n is the number of generations separating the individual from each known ancestor (Boichard et al., 1997). Calculations and estimates were done for rabbits born from 1992 to 2007 (REFPOP1992, REFPOP1993, ..., REFPOP2007, where **REFPOP** refers to the reference population), although they most often referred to REFPOP2007.
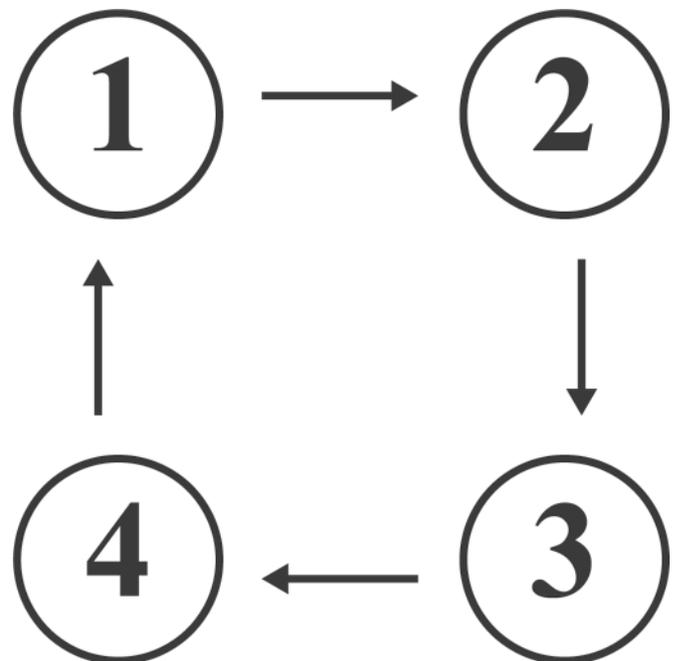

Figure 1. The circular mating scheme applied. (The arrows show the direction of male transfer.)

Inbreeding and Average Relatedness

The inbreeding coefficient, defined as the probability that the 2 alleles at any locus in an individual will be identical by descent (**IBD**), was calculated with respect to "total" pedigree information (F_i) and 4 generations of pedigree information (F_{i4}). The average relatedness coefficient (AR) is defined as the probability that an allele randomly chosen from the whole population belongs to a given animal (Goyache et al., 2003; Gutiérrez et al., 2003); this was calculated for all individuals.

The partial inbreeding coefficient (pF_i), defined as the probability that an individual will be autozygous (IBD) for an allele descended from a specified founder (Lacy et al., 1996; Lacy, 1997), was calculated using the gene dropping method (10^6 replications). The analyses included all 580 founders contributing to the inbreeding and provided complete decomposition of the "total" inbreeding coefficients for each reference population.

The ancestral inbreeding coefficient (F_{a_BAL}), defined as the probability that any allele in an individual has been autozygous (IBD) in previous generations at least once, was calculated by the stochastic approach (10^6 replicates) proposed by Suwanlee et al. (2007). According to Ballou (1997), F_{a_BAL} represents the cumulative proportion of the genome of an individual that has previously been exposed to inbreeding in its ancestors.

Effective Population Size

Family variance (fv) effective population size (N_e) was estimated from variances of family sizes, following the expression of Hill (1979):

$$\frac{1}{N_e} = \frac{1}{16noML}\left[2 + \sigma_{mm}^2 + 2\left(\frac{noM}{noF}\right)\text{cov}(mm,mf) + \left(\frac{noM}{noF}\right)^2\sigma_{mf}^2\right] + \frac{1}{16noFL}\left[2 + \left(\frac{noF}{noM}\right)^2\sigma_{fm}^2 + 2\left(\frac{noF}{noM}\right)\text{cov}(fm,ff) + \sigma_{ff}^2\right],$$

where noM and noF are the number of breeding males and females, L is the average generation interval, σ_{mm}^2 and σ_{mf}^2 are the variances of the male and female progeny of a male, respectively, σ_{fm}^2 and σ_{ff}^2 are the variances of the male and female progeny of a female, respectively, and cov(mm, mf) and cov(fm, ff) are the covariances of male and female progeny from each male and from each female, respectively.

The inbreeding effective population size, here denoted as N_elr, was estimated according to the method of Pérez-Enciso (1995) from the log regression of $(1 - F_y)$ over the date of birth and was further corrected by the length of the generation interval using the formula

$$1 - F_y = [1 - 1/(2N_e)]^y,$$

where F_y is the inbreeding coefficient of the individual at its date of birth y, using as reference the date of birth of the first individual in the data set, and y is the date of birth. The realized effective population size $\left(\overline{N_e}\right)$ was estimated according to the method of Cervantes et al. (2008a). First, following the method of González-Recio et al. (2007), we computed the individual increase in inbreeding (ΔF_i) for each individual in our REFPOP using the following expression:

$$\Delta F_i = 1 - \left(1 - F_i\right)^{1/g_e},$$

where F_i is the inbreeding coefficient of an individual and g_e is the number of equivalent generations known for that individual. The variable ΔF_i corrects the cumulative inbreeding coefficient F_i regarding the pedigree depth of the animal. Second, by using the average individual increase in inbreeding $\left(\overline{\Delta F}\right)$ of the REFPOP population (Gutiérrez et al., 2008), it is possible to compute the $\overline{N_e}$ by the relation

$$\overline{N_e} = \frac{1}{2\overline{\Delta F}}.$$

Probability of Gene Origin

The effective number of founders (f_e) is defined as the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study (Lacy, 1989) and is defined according to the following equation:

$$f_e = \frac{1}{\sum_{k=1}^{f} q_k^2},$$

where q_k is the proportion of the genes of the living descendant population contributed by founder k.

The previous method does not account for bottlenecks in the population, which is a major cause of gene loss due to AI. To take them into account, we also computed the effective number of ancestors (f_a), which is the minimum number of ancestors (not necessarily founders) needed to explain the complete genetic diversity of the population (Sölkner et al., 1998). The f_a is calculated by the same equation, but replacing the contributions of founders by the marginal contributions of ancestors (i.e., contributions not yet explained by another ancestor; for more details, see Boichard et al., 1997). The effective number of founder genomes (f_g), defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no loss of alleles occurred (Ballou and
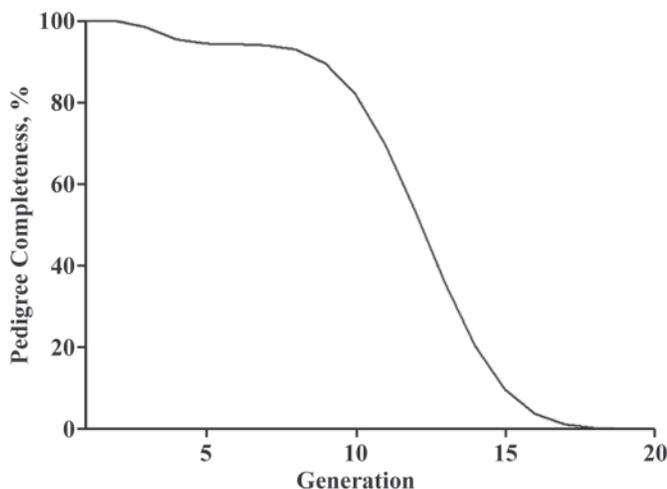
Figure 2. Average percentage of ancestors known per generation for Pannon White rabbits.
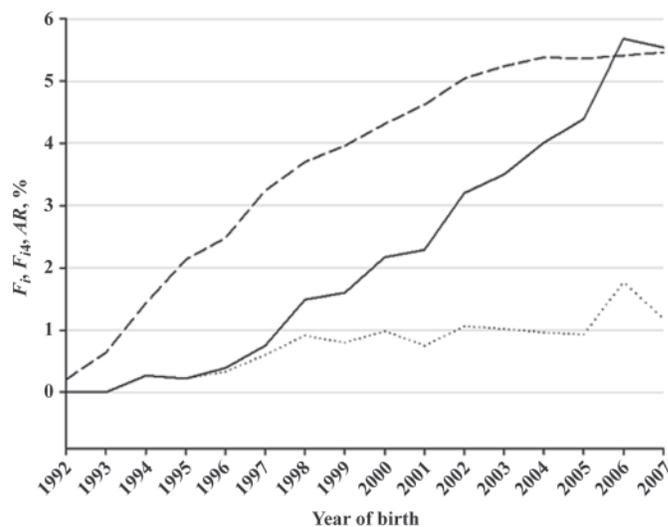

Figure 3. Trends for the mean inbreeding related to total (F_i; solid line) and 4-generation (F_{i4}; dots) pedigree, and the average relatedness (AR; dashes) for Pannon White rabbits.

Lacy, 1995), was calculated following the method of Caballero and Toro (2000).

Programs Used

Genetic variability and genetic similarity were measured using the software ENDOG, version 4.6 (Gutiérrez and Goyache, 2005). We also used GRain, version 2.0 (available from http://www.nas.boku.ac.at/1896.html or on request from roswitha.baumung@boku.ac.at), to calculate pF_i and f_{a_BAL}. Data manipulation, descriptive statistics, and simple statistics were obtained using various SAS procedures (SAS Inst. Inc., Cary, NC).

RESULTS

Generation Interval and Pedigree Information

Generation intervals, calculated across all pathways, are presented in Table 2. The mean generation interval for buck pathways was 1.40, whereas the mean generation interval for doe pathways was 0.40 yr shorter. The pedigree completeness is shown in Figure 2. The pedigree of PW was more than 90% complete until the ninth generation (see Figure 2), resulting in a large mean value for the number of known generation equivalents for REFPOP2007 (11.36).

Table 2. Descriptive statistics on the generation intervals (in years) for the 4 pathways in Pannon White rabbits born in 2007 (REFPOP2007)

Pathway	No.	Mean	SD
Buck-son	522	1.400	0.739
Buck-daughter	1,601	1.399	0.700
Doe-son	535	0.989	0.504
Doe-daughter	1,598	1.035	0.530
Overall	4,256	1.211	0.652

Inbreeding and AR

Trends for the mean F_i and the mean AR during a 15-yr-long period are presented in Figure 3. The mean F_i was constantly increasing, with the largest increase (1.29%) observed between 2005 and 2006. In contrast to F_i, the AR reached a value of approximately 5.4%, but has mainly stayed constant during the last 4 yr (Figure 3). For the REFPOP2007, we dissected individual inbreeding coefficients for the contribution of all 580 founders, of which 146 (25%) had a positive contribution. Considering those 146 founders in REFPOP2007, the average pF_i was 0.038%, with variance of 0.044%. The distribution of the pF_i of the 30 most contributing founders is presented in Figure 4. The 10 and 30 founders contributing the most to inbreeding explained a large part of the population inbreeding (i.e., 42.24 and 73.18%, respectively). For REFPOP2007 and REFPOP2004, the average ancestral inbreeding was 20.66 and 10.67%, respectively, with a variance of 16.84 and 3.77%, respectively, and a range of 13.62 and 5.71 to 35.91 and 15.40%, respectively.

Census and N_e

Trends in the census and N_e, estimated by 3 different approaches, are presented in Figure 5. The number of breeding PW rabbits increased up to 1997, when it reached a maximum of more than 500 rabbits. During the following 3 yr, the number of breeding PW rabbits was more than halved. From 2000 to 2005, the size of the PW rabbit population was relatively stable. From 2006, this number then decreased substantially and reached a minimum in REFPOP2007 (n = 169). The N_e for REFPOP2007 varied from 37.19 to 91.08, depending on the method of estimation.

Among the methods used, the weak point of the fv method is that it does not provide estimates for the

Table 3. Genetic contribution (%) of the 10 most influential ancestors to Pannon White rabbits born in 2007 (REFPOP2007)
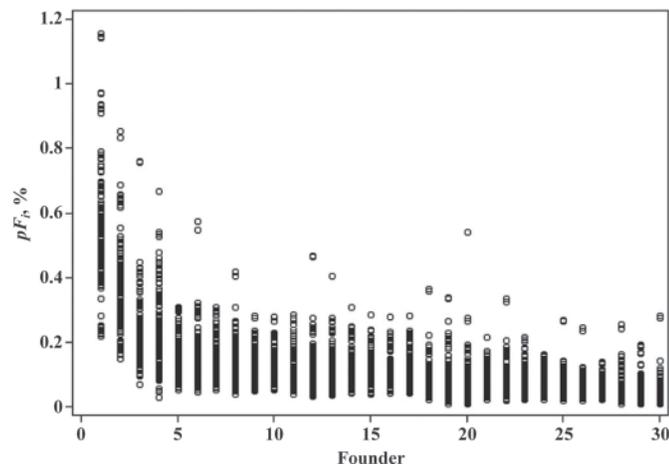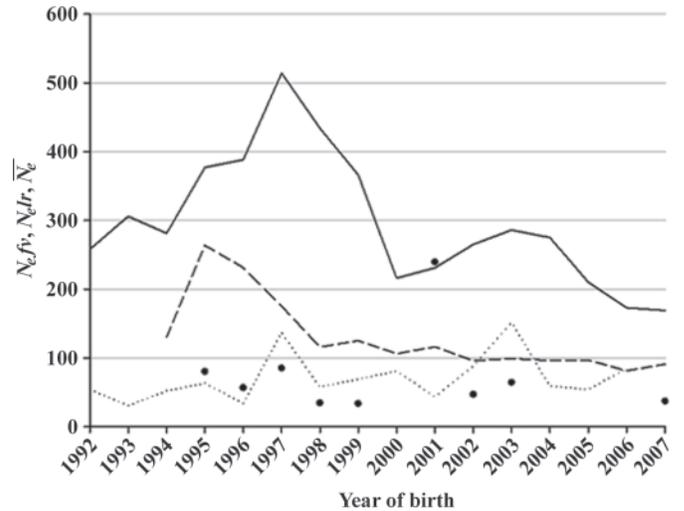
Ancestor identification	Birth year	Sex	Genetic contribution, %
200538519	2005	Male	8.80
200109343	2001	Male	7.96
199406850	1994	Male	6.90
200212057	2002	Male	5.63
200506325	2005	Female	5.53
199901085	1999	Male	4.95
200518447	2005	Male	3.95
200506675	2005	Female	3.54
200448283	2004	Female	3.53
200413105	2004	Male	3.19

Figure 5. Trends in the number of breeding rabbits (line), family variance effective population size ($N_e fv$; dots; Hill, 1979), inbreeding effective population size ($N_e lr$; black unconnected circles; Pérez-Enciso, 1995), and realized effective population size ($\overline{N_e}$; dashes; Gutiérrez et al., 2008) for Pannon White rabbits.

animals born in the last year. In most cases, the estimates calculated by the log regression approach were very close to those based on fv. However, the log regression method, as with all regression methods used to obtain N_e, demonstrated weak points and unreliability, attaining a value greatly dependent on recent changes in mating policy and being able to achieve even an unrealistic negative N_e after a period in which a planned mating (to minimize coancestry) was established. Thus, in the years when younger individuals were less inbred in PW, for example, in REFPOP2000, we were not able to provide any estimates (Figure 5).

Somewhat greater estimates were obtained when they were computed from ΔF_i. This method also showed unreliability in situations when the pedigree was not informative, but it performed reasonably well after pedigree completeness had been stabilized (Figure 5).
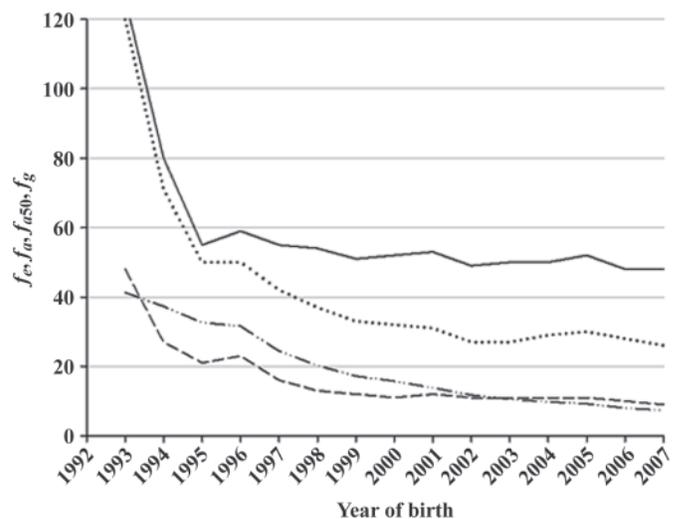
Probability of Gene Origin

Trends in probability of gene origin, f_e, f_a, f_{a50}, and f_g, are presented in Figure 6. Estimates decreased drastically in the first few years (from REFPOP1993 to REFPOP1995); later, however, they did not change significantly. Although the total number of founders in REFPOP2007 was 580, the contribution of the 10 main ancestors was large (Table 3).

To adjust for the influence of pedigree, we graphically compared the amount of inbreeding and pedigree quality obtained for PW rabbits with values obtained in horses, cattle, and pigs (Figure 7). The regression line (PW excluded) presents the mean F_i for domestic animal populations (i.e., horses, cattle, and pigs) with adjustments made for pedigree quality.

Figure 4. Distribution of the partial inbreeding coefficients (pF_i) for 30 founders with the greatest inbreeding contribution to Pannon White rabbits born in 2007 (REFPOP2007).

Figure 6. Trends in the probability of gene origin: effective number of founders (f_e; solid line), effective number of ancestors (f_a; dots), number of ancestors explaining the 50% of genetic variability (f_{a50}; dots and dashes), and effective number of founder genomes (f_g; dashes) for Pannon White rabbits.
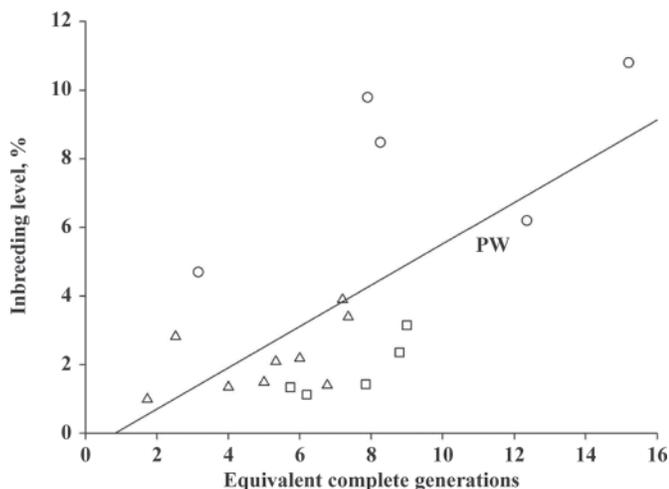
Figure 7. Comparison between mean equivalent complete generations and mean inbreeding coefficients (%) for Pannon White (PW) rabbits, as well as for other domestic animal populations: pig populations (squares; Baumung et al., 2002; Janssens et al., 2005), horse populations (circles; Zechner et al., 2002; Valera et al., 2005; Poncet et al., 2006; Royo et al., 2007; Cervantes et al., 2008b), and cattle populations (triangles; Baumung and Sölkner, 2002; Sorensen et al., 2005; Mc Parland et al., 2007).

DISCUSSION

Greater generation intervals calculated for sire-offspring pathways might be caused by the extensive use of reproductive techniques such as AI. Mc Parland et al. (2007) explained similar relationships observed in cattle populations by the longer use of proven semen, whereas longer generation intervals calculated for dam-offspring pathways were observed in domestic species (e.g., sheep), in which the use of AI is less widespread (Norberg and Sorensen, 2007).

The basic assumption in calculating the large number of coefficients derived from the pedigree is that founders are not related. Although this assumption is violated when a population is small and closed for a long time, it might be a more realistic assumption if founders are brought from diverse remote areas or if the number of founders is large (genetically), or both. Unfortunately, in most situations, information on the potential origin of the founders is scarce, and values across pedigrees with different information should be compared with caution (i.e., taking into consideration that founders are not related). The equivalent complete known generations of the PW were comparable with horse populations. Furthermore, the PW was positioned close to the presented regression line which we interpreted to mean the amount of inbreeding in PW was comparable with those of the majority of other domestic animal populations.

Unfortunately, the pedigree completeness of the French rabbit lines was not given (Kerdiles and de Rochambeau, 2002). Nevertheless, the inbreeding values observed in PW were much less than those observed by Kerdiles and de Rochambeau (2002) in the French rabbit strains 2066 (27%) and 1077 (22%). Although

greater inbreeding values were expected in French strains because they had pedigrees based on 20 generations, the differences among inbreeding values calculated on restricted pedigrees (4 generations) were very large. Thus, the mean "restricted" inbreeding coefficients, calculated for the whole data set, were equal to 4.24% for strain 1077 and 3.98% for strain 2066, and they exceeded the values obtained in this study substantially (0.70% for PW). Average relatedness indicates the long-term inbreeding (Goyache et al., 2003) and characterizes the mating system of a population. During the early 1990s, the mating of close relatives in PW rabbits was avoided and later was affected by the mating policy carried out. Average relatedness tended to be stable from 2002 on.

The contribution of founders to the inbreeding of individual rabbits of REFPOP2007 was small on average. However, for each inbred rabbit from 70 to 128 founders, 103 on average have contributed to the total inbreeding. As far as we are aware, there is neither theoretical speculation nor experimental evidence reporting the impact of the number of contributing founders to individual inbreeding on the magnitude of inbreeding depression. In general, under the assumption that each individual possesses several specific detrimental genes (Vogel and Matulsky, 1986; McGreevy and Nicholas, 1999), the pF_i is functionally related to the distribution of detrimental recessive defects in a population (for more details, see Man et al., 2007). Thus, a dissection of inbreeding (i.e., calculation of partial inbreeding coefficients) that sums to the total inbreeding does provide several possibilities for reducing recessive genetic defects, inbreeding depression, or both. For example, pF_i can be used in ranking founders with respect to their contribution to inbreeding depression (Gulisija et al., 2006; Casellas et al., 2008) or in detecting founders that are carriers of recessively inherited defects (Thompson and Morgan, 1989). Furthermore, calculation of partial inbreeding coefficients of hypothetical offspring might be used to avoid inbreeding arising from "bad" founders (i.e., founders with a greater contribution to inbreeding depression, known carriers of undesirable recessive genes, or both).

The idea behind f_{a_BAL} is that individuals with greater f_{a_BAL} values are expected to carry fewer detrimental genes. This concept does apply to the population level in a way that populations with greater mean ancestral inbreeding are expected to have a fewer number of recessive deleterious alleles (i.e., that purging of detrimental genes attributable to ancestral inbreeding might have occurred). Out of 25 mammalian populations analyzed by Ballou (1997), only 5 populations had greater f_{a_BAL} than were obtained in this study. The increased f_{a_BAL} obtained indicate potential purging of detrimental effects. Nevertheless, we should be aware that f_{a_BAL} values are strongly influenced by pedigree quality (completeness and length), which is an explanation for the sudden increase (double) observed in this study from REFPOP2004 to REFPOP2007.

The N_e has a direct relationship with the rate of inbreeding, fitness, and the amount of genetic variation lost because of random genetic drift (Falconer and Mackay, 1996; Caballero and Toro, 2000), and thus is also used as a criterion for characterizing the risk status of livestock breeds (FAO, 1998; Duchev et al., 2006). We estimated the effective size with 3 different approaches, each having its positive and negative aspects. The family size variance does not account for the possible structure of the population. The values obtained from the logarithmic regression approach are affected more by recent changes in the mating policy of the population. The use of logarithmic regression of inbreeding values to compute N_e is useful when the aim is to investigate the influence of temporal mating policies, although it is not possible to obtain valid estimates when inbreeding is decreased in the succeeding generation (Cervantes et al., 2008a). Hagger (2005) noted that a decrease in inbreeding occurs at the beginning of a crossing scheme, and the inbreeding N_e is a variable that does not account for crossbred animals. The downward trends in the amount of inbreeding obtained in some years in Irish cattle were caused by the import of germplasm (Mc Parland et al., 2007).

The $\overline{N_e}$ does not depend on the negative inbreeding trends (Cervantes et al., 2008a). In fact, $\overline{N_e}$ becomes a final measure of the accumulated drift, originating from the foundation of the population until the present, because it relies on all pedigree information available (Gutiérrez et al., 2008). The estimates obtained are almost stable when the known pedigree reaches approximately 5 equivalent generations (Cervantes et al., 2008). In this study, the estimates stabilized after 2002 (i.e., when the pedigree had reached the required informativeness).

All estimates related to the probability of gene origin decreased, and during the first years, the amount of decrease was the largest. As expected, the number of founder genome equivalents was the exception, where between 1993 and 1995 all variables were more than halved. This is in accordance with the report by Álvarez et al. (2007), who found that losses of genetic variability occurred very soon after setting up the breeding program because a significant number of founders did not give progeny to the following generation. Throughout the period analyzed (1993 to 2007), the number of founder genome equivalents decreased for almost 80% (REFPOP2007). However, although 50% were lost during the first 5 yr after the $\overline{N_e}$ was stabilized (in 2002), the additional loss was relatively small (10% of the initial value). Toro et al. (2000) reported a similar decrease (i.e., from 9.68 to 1.25; almost 90%) in a closed herd of Black Hairless Iberian pigs. In contrast, Kerdiles and de Rochambeau (2002) reported smaller decreases, 42.8% for the rabbit strain 1077 and 33.9% for the strain 2066 between the sixth and 20th generation, although this finding is not directly comparable with the results of the present study and with those of Toro et

al. (2000) because for the study by Kerdiles and de Rochambeau (2002), the largest decrease possibly occurred before generation 6. The favoritism of some relevant individuals is characterized by f_a/f_e and f_g/f_e describing the magnitude of bottleneck and drift. The estimates of f_a/f_e and f_g/f_e were 0.50 and 0.14, respectively. The unbalanced use of the breeding stock is apparent. The ratios observed were mostly greater than those of Austrian or Spanish pig populations (Rodrigáñez et al., 1998; Baumung et al., 2002), for which f_a/f_e and f_g/f_e varied from 0.22 to 0.34 and from 0.11 to 0.21, respectively. Rodrigáñez et al. (1998) found that the large magnitudes of bottleneck and drift for these pig populations were the result of the closed herd structure and the long evaluation period. The relatively favorable results of PW can be explained by the small sex ratio (1:2 and 1:3 during the last 2 yr) and by the effort to select breeding progeny from numerous bucks of all 4 groups. Contrary to the previous studies (Rodrigáñez et al., 1998; Baumung et al., 2002), Baumung and Sölkner (2002) reported increased f_a/f_e (0.97) and f_g/f_e (0.76) for Carinthian Blond cattle. The differences were due to the small complete generation equivalent of the Carinthian Blond cattle population (1.73). The disproportional use of some ancestors was evident from their genetic contribution.

A subdivided population structure is favored for maintenance of genetic diversity, whereas the number and size of the subpopulations and migration rates are critically important for a successful management plan (Wang and Caballero, 1999; Honda et al., 2002). Stochastically simulating a closed nucleus population, Terawaki et al. (1998) found that the creation of subpopulations can reduce inbreeding without a substantial loss of genetic gain. de Rochambeau et al. (2000) also suggested splitting populations into various reproduction groups, and described a mating scheme similar to the one applied to the rabbit groups in this study. Szőke et al. (2004) made similar suggestions when considering Bronze Turkey gene conservation.

The mating scheme analyzed in this study was relatively effective until recent years in controlling the inbreeding rate and loss of genetic variability of the rabbit population under study. However, the reduced census population size led to a substantial decrease in genetic variability in 2006. Overall, the results presented support the necessity of continuously monitoring PW rabbits with respect to the accumulation of genetic load and loss of genetic variability. The use of optimal contribution selection, as suggested by Meuwissen (2009), might be beneficial with respect to loss of genetic variability.

Nevertheless, we should be aware that there is no unique formula for how to proceed because the possibilities are numerous and sometimes controversial (Weigel, 2001), whereas the experimental evidence on the accumulation of detrimental genes under "optimizing" inbreeding schemes in livestock populations is scarce. To avoid the accumulation of genetic load, we further

suggest continuous analyses of inbreeding depression for reproductive and fitness traits with respect to founders. In addition, we propose identifying founders that are carriers of undesirable recessive genes. Those 2 analyses should be followed by a decomposition of inbreeding to the founder level and the use of hypothetical pF_i in mating schemes to avoid partial inbreeding of bad founders.

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