

# Investigation of genetic variability and inbreeding characteristics in a population of Zandi sheep

Farhad Ghafouri-Kesbi, Moradpasha Eskandarinasab, and Ahmad Hassanabadi

Department of Animal Science, University of Zanjan, Tabriz Road, P.O. Box 313, Zanjan 45195, Iran  
(e-mail: hassanabadi@znu.ac.ir). Received 16 October 2007, accepted 28 April 2008.

Ghafouri-Kesbi, F., Eskandarinasab, M. and Hassanabadi, A. 2008. **Investigation of genetic variability and inbreeding characteristics in a population of Zandi sheep**. *Can. J. Anim. Sci.* **88**: 409–417. The aim of the present study was to evaluate the genetic parameters and genetic trends for birth and weaning weights, and to quantify the inbreeding characteristics for a population of Zandi sheep. Genetic parameters from both single- and two-trait analyses were estimated using restricted maximum likelihood (REML) with animal models. Genetic trends were estimated by averaging estimated breeding values on year of birth. Full pedigree was analyzed for estimation of inbreeding characteristics. The results obtained confirmed relatively low additive genetic variation in the population, especially for weaning weight. Estimates of direct and maternal heritability were 0.12 and 0.20 for birth weight and 0.08 and 0.02 for weaning weight, respectively. Estimates of breeding values averaged by year of birth for birth weight and weaning weight increased over time. However, there was little genetic progress for birth weight ( $0.002 \text{ kg yr}^{-1}$ ), whereas the tendency for weaning weight was  $0.020 \text{ kg yr}^{-1}$ . Inbred animals consisted of 25% of the population. The effective population size ( $N_e$ ) was 66 individuals. The inbreeding rate per generation ( $\Delta F$ ) was 0.76%. The average value of inbreeding ( $F$ ) in the Zandi population was 1.05% and the average relatedness ( $AR$ ) coefficient reached 1.64% in the whole pedigree. A range of 2.84 to 4.01 yr was obtained for the average generation interval in different pathways. Selection of rams with the lowest  $AR$  was recommended for better management of inbreeding and avoidance of relative mating.

**Key words:** Sheep, genetic trends, heritability, inbreeding, average relatedness

Ghafouri-Kesbi, F., Eskandarinasab, M. et Hassanabadi, A. 2008. **Étude de la variabilité génétique et de la consanguinité d'une population de moutons Zandi**. *Can. J. Anim. Sci.* **88**: 409–417. L'étude devait évaluer les paramètres génétiques du poids à l'agnelage et au sevrage d'une population de moutons Zandi, et en quantifier la consanguinité. Les paramètres génétiques des analyses d'un et de deux caractères ont été estimés par la méthode du maximum de vraisemblance restreint (REML) sur des modèles animaux. Les tendances génétiques ont été évaluées par régression des valeurs reproductives, estimées selon l'année de naissance. Les sujets enregistrés ont été analysés afin d'en évaluer la consanguinité. Les résultats confirment une variation génétique par addition relativement faible, surtout pour le poids au sevrage. L'hérédité directe et l'hérédité maternelle s'établissent respectivement à 0,12 et 0,20 pour le poids à la naissance et à 0,08 et 0,02 pour celui au sevrage. La valeur reproductive moyenne pour le poids à l'agnelage et au sevrage estimée selon l'année de naissance augmente avec le temps. Toutefois, le poids à la naissance progresse peu sur le plan génétique ( $0,002 \text{ kg par année}$ ), tandis que pour le poids au sevrage, la tendance est de  $0,020 \text{ kg annuellement}$ . Les sujets consanguins représentaient 25 % de la population. La taille utile de la population ( $N_e$ ) est de 66 sujets. Le taux de consanguinité par génération ( $\Delta F$ ) s'élève à 0,76 %. La consanguinité moyenne ( $F$ ) de la population Zandi était de 1,05 % et le degré de parenté moyen ( $AR$ ) atteignait 1,64 % pour l'ensemble des animaux enregistrés. L'intervalle moyen entre les générations obtenu par différentes méthodes varie de 2,84 à 4,01 années. Les auteurs recommandent qu'on sélectionne des béliers à l' $AR$  le plus faible pour mieux gérer la consanguinité et éviter l'accouplement de sujets apparentés.

**Mots clés:** Moutons, tendances génétiques, hérédité, consanguinité, degré de parenté moyen

All around the world, sheep are maintained for different reasons, but in Iran sheep are raised mainly for meat production. According to Rashidi et al. (2008), about 35% of meat production in Iran, or 290 000 t annually, is from the production of sheep. Since the supply of meat from sheep does not meet demand, a breeding scheme is needed to increase the efficiency of sheep production by improving litter size, body conformation, lamb weight and milk yield. The Zandi sheep is one of the Iranian fat-tailed, medium-size breeds. They are adapted to the lowland areas of central Iran and are reared under a migratory system in Tehran Province. This breed is native to Iran, and due to its large

population (about 2 million head), there is considerable interest in genetically improving Zandi sheep for enhanced growth performance.

Success of a breeding program can be measured by actual change in breeding value expressed as a proportion of theoretical change of the breeding value mean for the character under selection (Jurado et al. 1994). Moreover, estimating genetic and environmental trends

**Abbreviations:** AI, artificial insemination; AR, average relatedness coefficient; BW, birth weight; WW, weaning weight

in populations allows assessment of the effectiveness of selection procedure and gives the opportunity for monitoring management conditions such as nutrition and health status (Kovac and Groeneveld 1990). Mixed model methodology has recently been used in the analyses of selection experiments (Meyer and Hill 1991), and the animal model methodology has become the most widely accepted approach to genetic parameter estimation and prediction of genetic effects.

However, populations subjected to selection may experience decreased genetic and phenotypic variances of the desired trait, because selection affords an opportunity to change gene frequency in a population by increasing the frequency of the advantageous alleles with additive effects. Therefore, heterozygosity and allelic diversity can be lost especially from small, closed, selected populations at a rapid rate. The loss of diversity and resulting increase in homozygosity may result in decreased production and/or fitness of inbred animals. Inbreeding occurs when related individuals are co-selected and when they or their offspring are subsequently mated to each other (Weigle 2001). Negative inbreeding effects, or inbreeding depression has been well documented in many populations for a variety of traits (Lamberson and Thomas 1984). In sheep, Ercanbrack and Knight (1981) found a slow response to selection for some productive traits within inbred lines. Therefore, it is important to estimate inbreeding in the populations undergoing selection to properly adjust the breeding process in an effort to avoid reduced performance from inbreeding.

The purpose of this study was to evaluate genetic variability of birth weight and weaning weight of the Zandi sheep. In addition inbreeding characteristics of the population were also investigated.

## MATERIALS AND METHODS

### Data Structure

Records of weight at birth and weaning and all available pedigree information of the Zandi sheep were obtained from the Zandi sheep breeding station (Khojir) from Tehran Province in central Iran. Weight records dated from February 1991 to April 2006, excluding 1993, for which no performance data were available on birth weight. The flock was established in the mid-1980s with animals purchased from different sheep farms in the region of the breeding station. Only pedigree information was recorded prior to 1991. The body weight information was recorded after 1990 and flock size increased slightly up to 450 breeding ewes in 2005.

In the project, ewes were first mated at about 18 mo of age and kept in the flock until being culled due to infertility or health problems, usually after five to six parities. Rams were used for 3 or 4 breeding years and kept separated from ewes; they were jointed in the mating season only. The mating season commenced in August of each year. Initially artificial insemination (AI)

was performed, and animals that did not conceive by AI were allocated to natural service. In the latter case, ewes were assigned to ram breeding groups with an average mating ratio of 10–15 ewes per ram. As ewes had different mating time, this followed with the long lambing season (December to May). At parturition, lambing date, number of lambs born, sex of lambs, and lamb birth weights were recorded. After lambing, lambs were kept with their dams for 1–3 d in separate pens depending on the number of lambs born. During the suckling period, lambs were kept indoors and fed supplemental grass hay and concentrate after 1 mo of age. The suckling program of the lambs lasted for 90 d on average. Ewes and weaned lambs grazed on the natural pasture of such genera as *Artemisia* and *Astragalus*. The flock was grazed during the day and housed at night. Pasture production is seasonal and depends on winter and spring precipitation. Range conditions were poor during the winter and, therefore, the sheep received supplemental feed for about 3 mo of the year. During this period, sheep had ad libitum access to grass hay and some concentrates.

Young rams were selected for increased growth performance using weaning weight and body conformation. The selection procedure for ewes was similar to that of rams. Animals were cared for in accordance with the Canadian Council on Animal Care (1993).

Weaning weights had been adjusted previously for 90 d of age as follow (Notter et al. 1975):

$$\begin{aligned} &[(\text{actual weight} - \text{birth weight})/\text{age in days}] \times 90 \\ &+ \text{birth weight} \end{aligned}$$

In the data editing stages, the data were screened several times and defective and doubtful data were deleted. In addition, four lambs that were born in 2006 were excluded from the estimation of (co)variance components. The number of birth weight and weaning weight records per each year are presented in Table 1. Pedigree information was retained during editing for use in an animal model. A brief description of the data set with some pedigree information for both birth weight (BW) and weaning weight (WW) is listed in Table 2.

### Statistical Analysis

Preliminary analyses were conducted using the GLM procedure of the SAS Institute, Inc. (2004) to identify nongenetic factors influencing lamb's weight. Factors considered in these models included year (15 classes, 1991 to 2005), season (winter; spring) sex (male; female), type of birth (single; twin; triplet) and age of dam at lambing in nine classes (2–10 yr old). All these fixed effects were significant ( $P < 0.05$ ) and were included in the models. An attempt was made to analysis the data using year-season contemporary groups, instead of year and season as separate fixed effects. Unfortunately, this analysis failed to converge, so these effects were fitted separately. Initially, univariate animal models were fitted to estimate

**Table 1.** Number of records per each year for birth weight (BW) and weaning weight (WW)

Trait	Year														
	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
BW	47	120	—	235	286	487	335	402	373	405	418	589	390	451	560
WW	37	76	218	216	193	362	272	288	224	227	300	286	303	367	484

the genetic parameters for each trait. By ignoring or including various combinations of maternal genetic (**m**) and maternal permanent environmental effects (**c**) in addition to direct additive genetic effect (**a**), four different models were used (Table 3). All models included an additive direct effect, and this was the only random factor in model 1. Model 2, included the maternal permanent environmental effect; and fitted as an additional random effect, uncorrelated with all other effects in the model. Model 3, included an additive maternal effect fitted as a second random effect. Model 4, was the same as model 3, but in this model, direct and maternal additive genetic effects were assumed to have joint covariance matrix  $\mathbf{G} \otimes \mathbf{A}$ , where  $\mathbf{G}$  is a  $2 \times 2$  genetic covariance matrix with animal and maternal additive genetic variance ( $\sigma_a^2$  and  $\sigma_m^2$ , respectively) on the diagonal and the direct-maternal additive covariance ( $\sigma_{a,m}$ ) on the off-diagonal,  $\mathbf{A}$  is the additive numerator relationship matrix and the symbol  $\otimes$  denotes the Kronecker's product matrix operator.

(Co)variance components were estimated by restricted maximum likelihood (REML) using a derivative-free algorithm fitting an animal model. Meyer's (2001) DFREML 3.1 package was used to estimate (co)variance components and associated genetic parameters. Principles of derivative-free restricted maximum likelihood (DFREML) have been described by Meyer (1989). Convergence of the REML solutions was considered reached when the variance of function values ( $-2 \log L$ ) in the Simplex was less than  $10^{-8}$ . The most appropriate model for each trait was selected based on the likelihood ratio tests (LRT).

(Co)variance components between traits were estimated from two-trait analyses, and all animals with

observations on birth weight and weaning weight were used. Breeding values of individual animals were estimated from two-trait analyses with best linear unbiased prediction (BLUP) methodology.

Deviation of selected parents from the mean of their birth cohorts, as an indication of selection differential, was estimated by subtracting the average of the selected sires and of the selected dams minus the mean of their birth cohorts.

The generation interval of four gametic pathways, sire to son ( $L_{mm}$ ), sire to daughter ( $L_{mf}$ ), dam to son ( $L_{fm}$ ), and dam to daughter ( $L_{ff}$ ), was obtained from records of birth dates of registered animals in each year and the birth dates of their sires and dams. The average generation interval ( $L$ ) was computed from:

$$L = \frac{L_{mm} + L_{mf} + L_{fm} + L_{ff}}{4}$$

### Methods of Measuring Inbreeding

By calculating  $F$ , individual inbreeding coefficients, a measure of the amount of genetic diversity that has been lost can be obtained by calculating the increase in inbreeding ( $\Delta F$ ) for each generation by means of the classical formula  $\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1})$ , where  $F_t$  is the average inbreeding at the  $i$ th generation. Using  $\Delta F$ , effective population size ( $Ne$ ) computed as:  $Ne = 1 / (2 \Delta F)$  for each generation having  $F_t > F_{t-1}$ .  $Ne$  is defined as the number of animals that would produce the observed rate of inbreeding if bred under ideal conditions in the current generation. Whatever the way to compute  $Ne$ , this parameter fits poorly in small populations with shallow pedigrees, giving an overestimate of the actual effective population size (Goyache et al. 2003). To better characterize this, we estimated three additional values of  $Ne$  by computing the regression

**Table 2.** Pedigree information, mean, standard deviation (SD), and coefficient of variation (CV) of birth weight (BW) and weaning weight (WW)

Item	Trait	
	BW	WW
No. of records	5098	3853
No. of animals	5638	4241
No. of sires with progeny	165	165
No. of dams with progeny	1419	1312
No. of grandsires with progeny	127	125
No. of granddams with progeny	805	594
Mean (kg)	4.12	19.69
SD (kg)	0.72	4.08
CV (%)	14	15

**Table 3.** The random (co)variance components used in the four models

Model number	Random effect <sup>z</sup>				
	$\sigma_a^2$	$\sigma_c^2$	$\sigma_m^2$	$\sigma_{a,m}$	$\sigma_e^2$
1	✓				✓
2	✓	✓			✓
3	✓		✓		✓
4	✓		✓	✓	✓

<sup>z</sup> $\sigma_a^2$ , direct additive genetic variance;  $\sigma_c^2$ , maternal permanent environmental variance;  $\sigma_m^2$ , maternal additive genetic variance;  $\sigma_{a,m}$ , direct-maternal additive genetic covariance;  $\sigma_e^2$ , residual variance.

coefficient ( $b$ ) of the individual inbreeding coefficient over: (i) the number of full traced generations; (ii) the maximum number of generations traced and (iii) the equivalent complete generations for each animals in pedigree data. The first is defined as the furthest generation in which all the ancestors are known. Ancestors with no known parent were considered as founders (generation 0). The second is the number of generations separating the individual from its furthest ancestor. The equivalent complete generations is computed as the sum over all known ancestors of the terms computed as the sum of  $(1/2)^n$  where  $n$  is the number of generations separating the individual to each known ancestor.

By considering the corresponding regression coefficient as the increase in inbreeding between two generations ( $F_t - F_{t-1} = b$ ), and consequently (assuming  $1 - F_{t-1} = 1$ );  $Ne = 1/2b$ . When the available information is scarce, these estimations can be useful to approximate the upper (using i), lower (using ii) and "real" (using iii) limits of  $Ne$  in the analyzed population (Gutierrez and Goyache 2005).

In addition, the inbreeding rate per generation was used to estimating inbreeding rate per year as follow:

$$\Delta F_{year} = \Delta F / L$$

Genealogical analyses on pedigree information were carried out using the program ENDOG (Gutierrez and Goyache 2005).

## RESULTS AND DISCUSSION

### Genetic Parameters

Estimates of genetic parameters from single-trait analyses, the basis of a more appropriate model, for BW and WW are given in Table 4. Direct heritability ( $h^2$ ) estimates for BW and WW were 0.12 and 0.08, respectively. These direct heritability estimates are lower than those reported for other Iranian sheep breeds. Zandie (2005) found a direct heritability of 0.16 for BW and 0.23 for WW in Kordi sheep. Miraei-Ashtiani et al. (2007), who worked on Sangsari sheep, reported direct heritability estimates of 0.33 and 0.17 for BW and WW, respectively. On the other hand, Rashidi et al. (2008) reported direct heritability estimates of 0.04 for BW and 0.27 for WW in Kermani sheep. Overall, literature estimates of heritability range from 0.04 (Rashidi et al. 2008) to 0.46 (Gizaw et al. 2007) for BW and from 0.06 (Ekiz 2004) to 0.47 (Gizaw et al. 2007) for WW. A number of factors such as breed of the animal, size and structure of the data used, genetic structure of the population, management and environmental conditions, and the method of estimating parameter would have affected the differences between estimations (Miraei-Ashtiani et al. 2007).

There are several reports on the significance of maternal effects on early growth in various sheep breeds (Ekiz 2004; Wilson et al. 2005; Szwaczkowski et al. 2006;

**Table 4. Estimates of genetic parameters from single-trait analyses<sup>a</sup>**

Trait	Model	$h^2$	$m^2$	$r_{a,m}$	$h_t^2$
BW	4	0.12 ± 0.03	0.20 ± 0.02	-0.17	0.18
WW	4	0.08 ± 0.04	0.02 ± 0.02	1.00	0.14

<sup>a</sup> $h^2$ , direct heritability;  $m^2$ , maternal heritability;  $r_{a,m}$ , direct-maternal genetic correlation;  $h_t^2$ , total heritability; BW, birth weight; WW, weaning weight.

Miraei-Ashtiani et al. 2007; Rashidi et al. 2008). Maternal effects are now widely recognized as important components of total phenotypic variation, particularly in mammals with long periods of maternal dependence. Maternal effects arise when the phenotype of a mother or the environment she experiences has a phenotypic effect on her offspring (Wilson et al. 2005). In general, maternal effects result from maternal traits controlled by her genotype and associated environmental factors. A portion of the maternal effects that have a genetic basis arise from allelic differences between individual mothers at loci influencing their performance (intra-uterine environments, milk production, mothering ability, etc.) and consequently affect their offspring phenotype (Wolf et al. 1998).

Estimates of maternal genetic effects as a proportion of phenotypic variance (maternal heritability,  $m^2$ ) were 0.20 and 0.02 for BW and WW, respectively. A higher estimate of maternal heritability than direct heritability for BW indicates that genes affecting maternal performance also have a greater influence on an individual's birth weight than do the genes carried by them. As maternal conditions during embryonic growth in the uterus strongly affect body weight at birth (Szwaczkowski et al. 2006), the higher maternal heritability for BW compared with WW was expected, which is in concordance with Miraei-Ashtiani et al. (2007), who reported a maternal heritability of 0.65 for BW and 0.08 for WW for Sangsari sheep. Wilson et al. (2005) reported that animal models which ignore maternal effects tend to overestimate direct heritability, which is in agreement with our findings, current estimates of direct heritability (under Model 4, containing maternal genetic effects) for BW and WW were lower than those obtained under simple additive animal model (Model 1, 0.33 and 0.15 for BW and WW, respectively).

In the present study, genetic correlation between BW and WW was positive and relatively high (0.74), suggesting that animal's genes acting at birth are similar to those acting at weaning (Fischer et al. 2004). Therefore, it is expected that animals with above-average BW would tend to be above average in genetic merit for WW. Hence breeding rams could be selected based on BW.

### Genetic Trends

Genetic trends of BW and WW for the duration of the experiment (1991–2005) are given in Figs. 1 and 2,

respectively. From 1991 to 2005, the mean of estimates of breeding values for BW and WW increased up to 0.03 and 0.33 kg, respectively (i.e., 0.002 kg yr<sup>-1</sup> for BW and 0.020 kg yr<sup>-1</sup> for WW). The observed genetic changes in our study are lower than those reported from previous studies. For instance, Hanford et al. (2005), who studied the response to long-term selection in Rambouillet sheep for birth weight and weaning weight, reported that during 1950–1998 the mean estimates of breeding values for birth weight and weaning weight increased over 0.9 and 8 kg, respectively (i.e., 0.018 and 0.16 kg yr<sup>-1</sup>, respectively). Moreover, Bosso et al. (2007) estimated annual genetic gain for Djallonke sheep in birth weight and weaning weight as 0.01 and 0.11 kg yr<sup>-1</sup>, respectively. Higher estimates were observed by Gizaw et al. (2007) for birth weight (0.038 kg yr<sup>-1</sup>) and weaning weight (0.27 kg yr<sup>-1</sup>) for Menz sheep in Ethiopia. However Zandie (2005) reported the annual genetic gain in Kordi sheep as 0.001 and 0.022 kg yr<sup>-1</sup> for BW and WW, respectively, which are closer to our findings.

When a trait such as early growth has a major maternal component, additional complexity is added to the characterization of genetic variability and response to selection (Legates 1972). Bradford (1972) stated that half of the response to selection for weaning weight could be attributed to maternal performance of the ewes. It has been argued that in the presence of maternal effects, direct heritability will not necessarily provide a useful measure of potential response of a trait to selection. A more appropriate measure is total heritability ( $h_t^2$ ), defined by Willham (1972) as:

$$(\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$$

Total heritability combines those co-variances that together explain the total additive variation present for a trait, replacing direct heritability when maternal genetic effects are present (Wilson et al. 2005).

Using the most appropriate model, total heritabilities for BW and WW were estimated as 0.18 and 0.14, respectively. These estimates confirm the existence of a

small additive genetic variation in the population. Therefore, the small additive genetic improvement in weight traits of Zandi sheep may be possible in selection programs. Shatt et al. (2004), who worked on two local Egyptian sheep, the Ossimi and Rahmani, reported higher genetic changes for body weight at 60, 120 and 180 d of age in Rahmani than in the Ossimi population. They reported that the higher genetic trends in Rahmani may be explained by the higher additive genetic variation in Rahmani compared with Ossimi population.

The contribution of maternal genetic effects in the selection response is determined with quality of direct-maternal genetic correlation ( $r_{am}$ ). Under a positive correlation between direct and maternal genetic effects, we will have a positive response to selection from both an offspring trait and on maternal performance for that trait. On the other hand, selection for lamb weight was also followed by improvement in milk production and maternal ability of ewes. All else being equal, the low maternal genetic effects on WW, followed by a small total heritability, is a limitation for any selection program toward increasing WW. In addition, due to small maternal genetic effects on WW, the strong positive correlation (+1.00) between direct and maternal genetic effects has little meaning. For BW, maternal genetic effect is 10 times larger than WW, but the correlation between direct and maternal genetic effects is negative (-0.2). With a large negative covariance between direct and maternal genetic effects, total progress is slow. As the direct component increases in one generation, a generation later most of that gain is offset by a decrease in the maternal component.

The genetic progress during the second half of the study was lower than during the first half. From 1991 to 1998, the genetic gains were 0.003 and 0.026 kg yr<sup>-1</sup> for BW and WW, respectively, whereas from 1998 to 2005 annual genetic gains for BW and WW were reduced to 0.001 kg yr<sup>-1</sup> for BW and 0.012 kg yr<sup>-1</sup> for WW. Table 5 shows the deviations, selection differentials, of selected sires and dams from their birth cohorts. These results clearly show that selection differentials, especially for

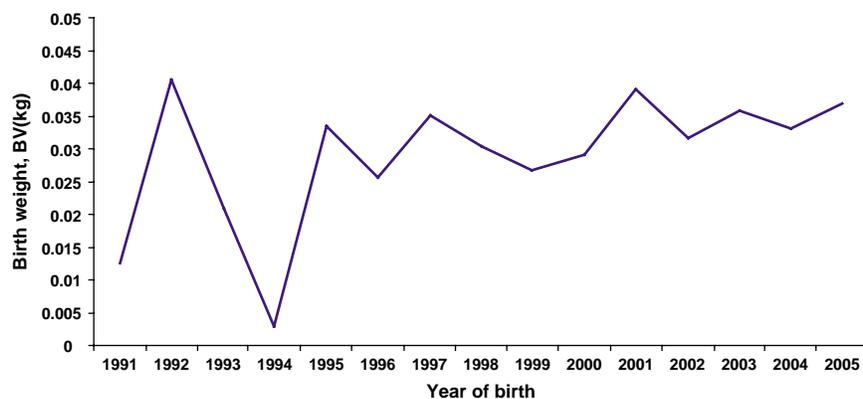


Fig. 1. Genetic trend for birth weight.



Fig. 2. Genetic trend for weaning weight.

sires, decreased after 1998 for both BW and WW, resulting in a decreased response to selection. Alternatively, the estimates were considerably lower in dams than in sires, indicating the absence of a selection strategy or, at least, low selection intensity on the dam side. Therefore, nearly all of the observed selection response was achieved through selection among the rams. Effective selection among the ewes is also required for increasing the efficiency of selection.

### Inbreeding Characteristics of the Population

The effect of inbreeding on response to selection is well known. High levels of inbreeding reduce genetic variance and subsequent selection response. Selection either on phenotype (mass selection) or on BLUP increases inbreeding in the population (Quinton et al. 1992). Especially where animals are selected based on their estimated breeding values (EBVs), groups of relatives often have similar EBVs and, therefore, they are

selected or culled as a group, thereby increasing relatedness in the population.

Here, the effective population size was  $N_e = 66$ . The effective size of a population is a parameter central to understanding evolution in small populations, because the magnitude of this parameter determines the genetic effects of both inbreeding and genetic drift (Falconer and Mackay 1996). Therefore, estimation of  $N_e$  would be useful to understanding of the risk of selection. The inbreeding rate per generation ( $\Delta F$ ) was equal to 0.76% and the resulting  $\Delta F_{\text{year}}$  was equal to 0.22%. Nevertheless, the resulting  $\Delta F$  is in accordance with Bijma (2000), who advises that the inbreeding level in a zootechnic population should increase at most 0.5 to 1% per generation. In the planning stage of a breeding program, estimations of  $\Delta F$  in whole pedigree was 1.05% and the average relatedness coefficient ( $AR$ ) was 1.64%. Inbred animals were 25% of the population. Their mean  $F$  was low at 4.21%, and their mean  $AR$  was 2.47%.

$F$  and  $AR$  by year of birth for duration of the study are illustrated in Fig. 3.  $F$  was 0.00 from the foundation of the herdbook to 1992. In this year, the number of animals with unknown parents registered in the herdbook decreased considerably. After 1994 inbreeding increased sharply and reached to a peak of 4% at 2000. This result occurred because of the small number of Zandi individuals available, and the over use of certain individuals as parents. Inbreeding dropped sharply after 2000 due to the breeding strategy. In the station, each ram was assigned to a group of ewes for 2 yr and afterwards replaced with a new unrelated ram. This breeding strategy, although it has successfully decreased the rate of inbreeding, did not completely eliminate inbreeding since the inbreeding level increased from 2001 to 2005. The use of AI, which is in progress, has also increased relatedness within populations by reducing the effective number of parents. In the long term, inbreeding can be better controlled by the selection strategy than by the mating strategy (Portolano

Table 5. Estimates of deviation of selected sires and dams from the mean of their birth cohorts (kg) for birth weight (BW) and weaning weight (WW)

Year	Trait					
	BW			WW		
	Sire	Dam	Mean	Sire	Dam	Mean
1991	0.461	0.013	0.237	0.109	-0.311	-0.100
1992	0.235	0.119	0.177	-0.730	0.157	-0.286
1994	0.467	0.011	0.239	2.472	0.023	1.248
1995	0.593	0.020	0.307	2.711	-0.226	1.242
1996	-0.313	0.000	-0.157	-1.142	0.343	-0.399
1997	0.211	-0.103	0.054	1.592	0.139	0.865
1998	0.578	0.054	0.315	2.535	0.755	1.645
1999	0.170	0.035	0.103	1.195	0.001	0.598
2000	0.054	0.007	0.030	0.752	0.151	0.452
2001	0.045	0.178	0.112	0.924	0.606	0.765
2002	0.227	-0.032	0.097	0.602	0.439	0.520
2003		0.036			-0.052	

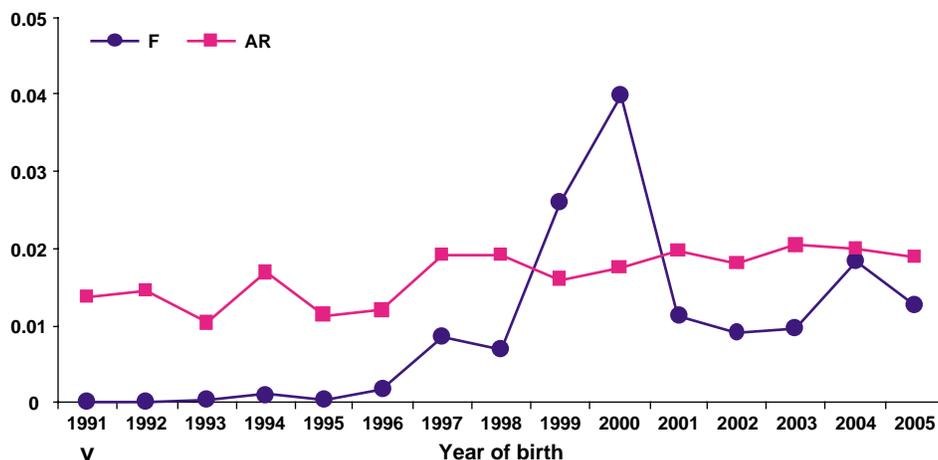


Fig. 3. Increase of inbreeding ( $F$ ) and average relatedness ( $AR$ ) by year of birth.

et al. 2004). Currently, selection tools are available to consider the inbreeding rate in the selection strategy of small populations (Meuwissen 2002).

$AR$  was higher than 1% throughout the study period, indicating that individuals were genetically related. The  $AR$  of each individual is defined as the probability that an allele randomly chosen from the whole population in the pedigree belongs to a given animal (Gutierrez and Goyache 2005). The average inbreeding coefficient of a population is frequently used as a measure of its level of homozygosity (Gutierrez et al. 2003). When the number of animals with unknown parents registered in the herdbook is high and/or when a population is open to the introduction of new individuals with unknown pedigree, we could not adequately assess the actual level of inbreeding in a population. In addition, registration of the high number of founders in the herdbook kept inbreeding at a relatively low level. The computation of the individual coefficient of inbreeding is highly sensitive to the quality of the available pedigree information, thus making this parameter difficult to interpret (Goyache et al. 2003). In such a situation, an unobserved genetic drift may lead to losses in genetic diversity. Under this condition,  $AR$  can be used as an alternative or complement to  $F$  to predict the long-term inbreeding of a population, and can be very interesting for monitoring small populations (Goyache et al. 2003). In the present study  $AR$  reached 1.5% in 1992 before the genetic relationship existing between individuals could be measured as inbreeding.  $AR$  can be used as a measure of inbreeding of the whole population, as it takes into account both the inbreeding and the co-ancestry coefficients (Gutierrez and Goyache 2005). Therefore, in small populations and in situations of low-quality pedigree information, using  $AR$  increases the available information and gives an opportunity for better planning the mating programs. In this case, Goyache et al.

(2003) recommended using rams showing the lowest  $AR$  coefficients for avoidance of relative mating.

There is evidence that traits of low heritability are more adversely affected by inbreeding than highly heritable traits (Ercanbrack and Knight 1981; Lamberson and Thomas 1984). For instance, Ercanbrack and Knight (1981) compared response to selection in inbred lines for productive traits at weaning in Rambouillet, Targhee and Columbia sheep, and reported that traits of low to moderate heritability (weaning weight, body type and body condition) were generally depressed more than traits of higher heritability (staple length, face cover and wool grade). Highly heritable traits are primarily affected by additive genetic effects, whereas less heritable traits are affected by dominance effects (Falconer and MacKay 1996). According to Fu and Ritland (1994), inbreeding depression is caused by dominance; hence, traits of low heritability tend to show more inbreeding depression. Therefore, at the same levels of inbreeding, WW would be affected more than BW, and this could be another limitation for selection on WW; as selection proceeds, a portion of the response will be offset by inbreeding.

The average generation interval ( $L$ ) was 3.45 yr (Table 6), which was in the range reported in the other literature (Goyache et al. 2003; Shatt et al. 2004). In the sire-offspring pathway, the generation interval was lower because sires were replaced earlier than dams.

Table 6. Generation intervals (in years) for the four pathways

Pathway	N	Years
Ram-son	147	2.84
Ram-daughter	997	2.97
Dam-son	150	3.96
Dam-daughter	1117	4.01
Average		3.45

Since decisions about the mother of a ram required sufficient information on the ewe's performance, at least two lambs (Goyache et al. 2003), the longest estimate for dam-son pathway will be expected. Prolongation of the generation interval can be used with the aim of increasing the number of animals and thus to increase the effective population size and to reduce the genetic drift. However, in order to achieve an optimum selection response, a reasonable choice of generation interval must be achieved (Portolano et al. 2004).

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