Population genetic analysis of White Park Cattle in Germany

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Abstract

The population of White Park Cattle in Germany is composed of 11 males and 33 females. This group of cattle has been analysed with regards to generation intervals, coancestry, and inbreeding on the basis of three generations of ancestors. The average interval between the current and the parental generation amounts to seven years. The average coefficient of coancestry in the population is estimated to be 18% and the average degree of inbreeding at 16%. The rate of inbreeding in the last generation is approximately 12%. These values exceed those reported for most breeds of production animals.

Keywords: White Park Cattle, generation interval, relationship, inbreeding, rate of inbreeding

Zusammenfassung

Populationsgenetische Analyse der White Park Cattle-Population in Deutschland

Die aus 11 männlichen und 33 weiblichen Tieren bestehende White Park Cattle-Population in Deutschland wurde auf der Basis von drei Vorfahrengenerationen hinsichtlich ihrer Generationsintervalle sowie der Verwandtschafts- und Inzuchtverhältnisse untersucht. Das durchschnittliche Generationsintervall zwischen der aktuellen und ihrer Elterngeneration beträgt annähernd sieben Jahre. Der mittlere Verwandtschaftskoeffizient wurde mit 18%, der mittlere Inzuchtkoeffizient mit 16% geschätzt. Mit der aktuellen Generation stieg die Inzucht um ca. 12% an. Diese Werte liegen weit über jenen, die von anderen Nutztierrassen bekannt sind.

Schlüsselwörter: White Park Cattle, Generationsintervall, Verwandschaft, Inzucht, Inzuchtkoeffizient

Introduction

White Park Cattle are a horned cattle breed which is white with coloured points including the ears, nose, rims of eyes, teats, and feet. The intensity of these markings varies from herd to herd. White Park Cattle are considered primarily a beef breed and selected for this purpose. Sometimes they have also been kept for dual purposes, because some herds

have been used for milk production. They are reported to be well adapted to non-intensive production systems (Ancient White Park Cattle Society of North America 2008). However, the primary aim of breeding and keeping of this endangered breed is to conserve a very ancient genetic resource.

These animals of medium size are known to be easily satisfied, robust, long living, easily calving and late maturing. Adult cattle are weighing about 400-500 kg (cows) and 600-700 kg (bulls), respectively, and reach a withers height of about 130 cm (cows) and 137 cm (bulls), respectively (ANONYMOUS 2008).

The origin of the White Park Cattle is rather obscure; their blood-group alleles seem to be unique among cattle breeds of Western Europe (CHILLINGHAM CATTLE ASSOCIATION 2000). The earliest references to the White Park type are found in the pre-Christian Irish epics in which white cattle with coloured points were often mentioned as a special breed. With the arrival of the Romans the Druids and their herds were pushed to the northern and western fringes of Britain and Ireland. It is in these areas that the ancient herds of White Park Cattle in the pre-sixteenth century were found, although none remain in Ireland (ALDERSON 2008). Living as a free-ranging population and being hunted as game animals they once covered the British isles before several herds were enclosed within various large parks in the thirteenth, fourteenth and fifteenth centuries by the nobility, mostly serving as game animals. The Dynevor herd originating in the time before 1200 is probably the oldest of these herds. The origin of the Chartley and Chillingham herd in England and the Cadzow herd in Scotland can be traced back to the middle of the thirteenth century (ALDERSON 2008).

At the beginning of the nineteenth century still more than a dozen of White Park Cattle herds existed. Only six of these herds survived, namely, those of Dynevor, Woburn, Whipshade, and Cadzow which are domestic herds, and those of Chillingham and Vaynol, which have survived as semi-feral herds.

The genetic data bank of EAAP (European Association for Animal Production) reported the number of White Park Cattle in the United Kingdom in 1997 as 31 bulls and 367 cows. The Ancient White Park Cattle Society of North America estimated a worldwide population of approximately 500 purebred females in 79 herds, plus bulls and young stock. The current status of the breed is regarded as critical (TGRDEU 2001)

Over the past 50 years, White Park Cattle have been exported to the United States of America, Denmark, Australia, Canada and Germany where new herds have been established.

In Germany the largest herd exists in the zoological garden of Arche Warder in Schleswig-Holstein in northern Germany; additionally, there are some smaller herds.

Material and methods

For the analysis of the White Park population in Germany the data (name, herd book number, date of birth, date of exit of the probands and all their ancestors) of 44 animals (11 males, 33 females) from four herds (number of October 2008) were available.

The program OPTI-MATE 3.85 of WREDE and SCHMIDT (2004) was used. As it is based on the pedigree method, the calculations had to be limited to only three generations of ancestors, because the data of elder generations are very incomplete.

Figure 1
White Park Cow (Arche Warder – Zentrum für alte Haus- und Nutztierrassen e. V., Warder, Germany),
Photo: Heike Rudolph
*White Park Kuh (Arche Warder – Zentrum für alte Haus- und Nutztierrassen e. V., Warder, Deutschland), Foto:
Heike Rudolph*

The date of birth of the animals and of their ancestors was necessary to calculate intervals between generations, which means the average age of parents when giving birth to their offspring used for future breeding. The contribution GI_i of an animal I to the mean generation interval of a population can be estimated by the following equation:

$$GI_i = \frac{\sum_{j=1}^{k} t_{ij} \cdot n_{ij}}{\sum_{j=1}^{k} n_{ij}} \tag{1}$$

where is n_{ij} the number of offspring of the i-th animal at the j-th birth, t_{ij} the age of the i-th animal at the j-th birth and k the number of births of the i-th animal.

The average generation interval GI of the population results from the mean of all tested breeding animals:

$$GI = \frac{\sum_{i=1}^{N} GI_i}{N} \tag{2}$$

where is N the number of breeding animals in the population.

The coefficients of coancestry and inbreeding of the individuals have been estimated utilizing the pedigree method created by WRIGHT (1923).

The coefficient of coancestry R_{XY}, as a measure of the degree of relationship, represents the probability that two randomly choosen alleles at any locus in two individuals (X,Y) are identical by descent. It can be estimated as follows:

$$R_{XY} = \frac{\sum_{i=1}^{n} \left[\left(\frac{1}{2}\right)^{n_{1_i}+n_{2_i}} \cdot \left(1+F_{A_i}\right) \right]}{\sqrt{(1+F_X) \cdot (1+F_Y)}} \tag{3}$$

where is n_{1_i} the number of generations between X and the common ancestor A_i, n_{2_i} the number of generations between Y and the common ancestor A_i, F_{A_i} the coefficient of inbreeding of the common ancestor A_i, F_X the coefficient of inbreeding of X, and F_Y the coefficient of inbreeding of Y.

The mean of all coefficients of coancestry gives the average degree of relationship $\bar{R}$ in the population. Coefficients of coancestry vary between 0 and 1 or 0% and 100%.

The inbreeding of an animal X is measured by the coefficient of inbreeding. It represents the probability that both alleles at any gene locus are identical by descent. Of course, inbreeding requires the kinship of both parents. Coefficients of inbreeding are estimated by the following equation:

$$F_X = \sum_{i=1}^{n} \left[\left(\frac{1}{2}\right)^{n_{1_i}+n_{2_i}+1} \cdot \left(1+F_{A_i}\right) \right] \tag{4}$$

where is n_{1_i} the number of generations between X and the common ancestor A_i, n_{2_i} the number of generations between Y and the common ancestor A_i and F_{A_i} the coefficient of inbreeding of the common ancestor A_i.

The mean of the coefficients of inbreeding of all animals in the population corresponds to the average coefficient of inbreeding $\bar{F}$ of the population. Coefficients of inbreeding vary between 0 and 1 or 0% and 100%.

Using the pedigree method, incomplete pedigrees result in incorrect estimates of the coefficients of inbreeding. To minimize this underestimation the coefficients of inbreeding have been corrected by an index of completeness CI (SCHMIDT 2000), which gives the possibility to quantify the undervaluation of inbreeding independent of the number of unknown ancestors. All unknown ancestors, their position in the pedigree, and the distribution of the known male and female ancestors on the father's and mother's side of the pedigrees are considered:

$$CI = \frac{\left(C_{pat.m} \cdot C_{mat.m}\right) + \left(C_{pat.f} \cdot C_{mat.f}\right)}{2} \tag{5}$$

where is $C_{pat.m/pat.f}$ the completeness of the male/female ancestors on the father's side and $C_{mat.m/mat.f}$ the completeness of the male/female ancestors on the mother's side.

As there are no female ancestors in the first paternal generation and no male ancestors in the first maternal generation of ancestors two different formulas are needed to quantify the completeness of the four lineages:

$$C_{pat.m/mat.f} = \frac{1}{d} \cdot \sum_{i=1}^{d} a_i \tag{6}$$

$$C_{pat.f/mat.m} = \frac{1}{d-1} \cdot \sum_{i-1}^{d} a_i \tag{7}$$

where is d the number of generations of ancestors and a_i the portion of known ancestors in the i-th generation.

The importance of all ancestors as contributors to the average inbreeding of the current population was analysed by calculating their relative fraction of the mean of the population's inbreeding.

For the development of a population, the rate of inbreeding is substantial. It means the population's increase of inbreeding per generation or the increase of the population's average coefficient of inbreeding per generation. For this parameter, the so-called effective size of a population (N_e) is decisive, that is the number of individuals of an »ideal population« (population with random mating and equal sex distribution) which is equivalent to the actual population. The effective size of a population N_e results from:

$$N_e = \frac{4 \cdot N_m \cdot N_f}{N_m + N_f} \tag{8}$$

where is N_m the number of breeding males and N_f the number of breeding females of the population. The relationship between the effective size N_e of a panmictic population and the expected rate of inbreeding ΔF is as follows:

$$\Delta F = \frac{1}{2 \cdot N_e} \tag{9}$$

The rate of inbreeding for preceding generations has been estimated by the following formulas:

$$\Delta F_1 = \frac{F_t}{n-1}$$

(10)

where is ΔF_1 the mean rate of inbreeding in all generations of ancestors included and F_t the mean coefficient of inbreeding of the current generation. ΔF_{1c} is the mean rate of inbreeding in all generations of ancestors included, based on coefficients of inbreeding corrected by coefficients of completeness.

$$\Delta F_2 = \frac{F_t - F_{t-1}}{1 - F_{t-1}}$$

(11)

where is ΔF_2 the rate of inbreeding in the last generation, F_t the mean coefficient of the current generation, and F_{t-1} the mean coefficient of inbreeding of the parental generation. ΔF_{2c} represents the rate of inbreeding in the last generation, based upon the coefficients of inbreeding corrected by the coefficients of completeness.

Results

Generation intervals

The generation intervals between parents and individuals of the current generation amounts to about seven years, the value of the males being about 1.4 years higher than that of the females (Table 1).

Table 1
Mean generation intervals and their ranges (years)
Durchschnittliche Generationsintervalle und deren Schwankungsbreite (Jahre)

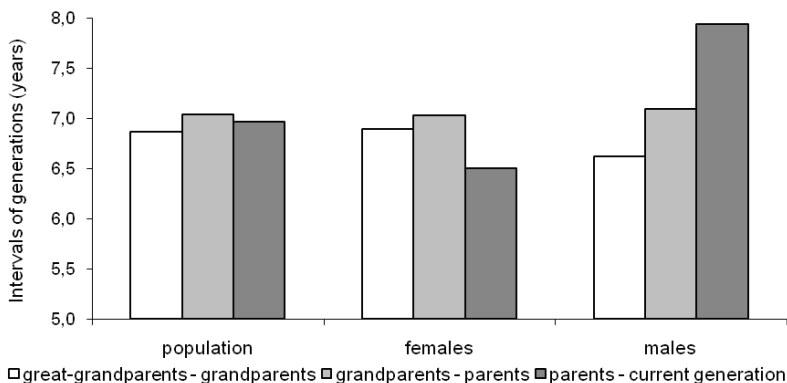| Path	Population		Females		Males	
Parents - offspring	6.96	(2.46-11.46)	6.50	(2.46-10.86)	7.94	(5.32-11.08)
Fathers - offspring	6.56	(2.31-11.21)	5.86	(2.31-10.01)	8.10	(6.40-11.21)
Mothers - offspring	7.36	(2.61-11.71)	7.14	(2.61-11.71)	7.78	(4.23-10.94)

Figure 2
Course of mean intervals of generations during successive generations
Entwicklung der mittleren Generationsintervalle im Verlauf der Generationen

Figure 2 shows that the generation intervals within the total population and the female population varied more or less in the course of preceding generations. The intervals of generation of the male population, however, has consistently increased.

Genetic relationships within the population

The average coefficient of coancestry within the population is approximately 18 %. It is less between the females but much higher between the males (Table 2). The maximum is 87.50 %. About 42 % of all the cases within the population (nearly 50 % within the females but only 18 % within the males) are without any relationship.

Table 2
Coefficients of coancestry (above) and their distribution (below, %)
Verwandtschaftskoeffizienten (oben) und deren Verteilung (unten, %)

	Population	Females	Males
Mean coefficient of relationship $\bar{R}$, %	18.19	15.75	25.09
Maximum coefficient of relationship R_{max}, %	87.50	87.50	78.13
Mean index of completeness, %	53.48	49.23	66.76
R = 0	41.65	49.43	18.18
0 < R ≤ 10	4.86	4.92	1.82
10 < R ≤ 20	11.84	9.09	20.00
20 < R ≤ 30	16.17	14.39	23.64
30 < R ≤ 40	9.83	8.14	18.18
40 < R ≤ 50	8.03	7.20	12.73
50 < R ≤ 60	3.17	2.84	0.00
60 < R ≤ 70	2.64	2.65	1.82
70 < R ≤ 80	1.37	0.95	3.64
80 < R ≤ 90	0.42	0.38	0.00

Coefficients of inbreeding

The average coefficient of inbreeding $\bar{F}$ in the total population equals approximately 9 %. Within the male population it is nearly 10 %. The maximum value is 37.50 % (Table 3). After correction by the indices of completeness the corrected coefficient of inbreeding $\bar{F}_c$ increases to about 16-17 %. Yet more than 40 % of all animals are not inbred.

Animals contributing to inbreeding

In Table 4 animals contributing to inbreeding specified with their number of ties causing the inbreeding of the actual population and their contribution to the average inbreeding of the population are listed. The sire Hestehave Ursus stands out as a very important contributor to inbreeding. More than 40 % of inbreeding inherent in the population can be traced back to this ancestor. Other significant contributors to inbreeding are the sires Nelson, Gerhard, Chartley, and Quartermaster, and the cows Sally and Tempelson Violet.

Rate of inbreeding

During the preceding three generations the increase of inbreeding ΔF_1 of the total population amounted to 4.62 %, within the females to 4.50 %, and within the males to 4.97 % (Table 5). Considering the index of completeness the values changed to much higher levels (ΔF_{1c}). The rate of inbreeding increased within the total population and within

the female population to nearly 8%, and to nearly 9% within the male population. The rate of inbreeding ΔF_2 between the generation of parents and the current generation is higher than that between the means of all former generations of ancestors, but after having performed the correction by indices of completeness of the pedigrees the rate of inbreeding leaps up to a very high level of 11-12% (ΔF_{2c}).

Table 3
Degrees of inbreeding (above) and their distribution (below, %)
Inzuchtkoeffizienten (oben) und deren Verteilung (unten, %)

	Population	Females	Males
Mean coefficient of inbreeding $\bar{F}$, %	9.23	9.00	9.94
Maximum coefficient of inbreeding F_{max}, %	37.50	37.50	28.13
Mean index of completeness $\bar{CI}$, %	57.96	58.21	57.20
Corrected mean coefficient of inbreeding $\bar{F}_C$, %	15.93	15.46	17.38
F = 0	43.18	42.42	45.45
0 < F ≤ 5	2.27	3.03	0.00
5 < F ≤ 10	22.73	24.24	18.18
10 < F ≤ 15	4.55	6.06	0.00
15 < F ≤ 20	9.09	9.09	9.09
20 < F ≤ 25	6.82	3.03	18.18
25 < F ≤ 30	6.82	6.06	9.09
30 < F ≤ 35	2.27	3.03	0.00
35 < F ≤ 40	2.27	3.03	0.00

Table 4
Animals contributing substantially to inbreeding
Inzuchtverursacher

Name	Sex	Born	Number of ties	Contribution to mean inbreeding, %
Population				
Hestehave Ursus	male	1989	22	43.85
Nelson	male	unknown	9	15.39
Sally	female	1994	3	12.31
Gerhard	male	2000	2	12.31
Chartley Quartermaster	male	unknown	9	8.46
Tempelson Violet	female	1988	6	7.69
Females				
Hestehave Ursus	male	1989	17	42.11
Nelson	male	unknown	7	16.84
Sally	female	1994	3	16.84
Tempelson Violet	female	1988	5	8.42
Gerhard	male	2000	1	8.42
Chartley Quartermaster	male	unknown	6	7.37
Males				
Hestehave Ursus	male	1989	6	49.49
Gerhard	male	2000	1	21.99
Chartley Quartermaster	male	unknown	4	11.34
Nelson	male	unknown	2	11.00
Tempelson Violet	female	1988	1	5.50
Dynevor Claudius	male	unknown	1	0.69

Table 5
Rate of inbreeding, %
Inzuchtraten, %

	Population		Female		Male	
	ΔF	N_e	ΔF	N_e	ΔF	N_e
ΔF_1	4.62	10.83	4.50	11.12	4.97	10.06
ΔF_{1c}	7.97	6.28	7.73	6.47	8.69	5.75
ΔF_2	7.12	7.02	7.34	6.81	7.04	7.10
ΔF_{2c}	11.17	4.48	11.78	4.25	12.05	4.15

Discussion

Only three generations of ancestors could be included into the present analysis because the pedigrees of many animals are incomplete. Moreover, the date of birth of many ancestors is unknown. This prevents their inclusion in the calculation of generation intervals. These inherent insufficiencies have to be considered when drawing conclusions from the analysis.

Generation intervals

The intervals of generations between male and female populations must be considered separately. Within dairy and beef breeds the bulls are rather young when they are recruited for mating or artificial insemination. In the case of White Park Cattle, however, sires begin mating at a different age. Therefore, the generation interval of the male line is not as important in contrast to that of the female line. In order to realize high breeding progress within efficiently bred populations, short generation intervals are advantageous. Within small populations with the main aim of conservation, long generation intervals are advantageous in order to minimize the increase of inbreeding per unit of time, as shown in the following equation:

$$\Delta F / year = \frac{\Delta F / generation}{GI} \qquad (12)$$

where is *ΔF/year* the rate of inbreeding per year, *ΔF/generation* the rate of inbreeding per generation, and *GI* the generation interval (years).

In the present investigation the generation intervals between mothers and their offspring appear rather favourable (7.4/7.1/7.8 years). From this equation, it is clear, that in order to effect a further increase, it would be preferable to select the later born female offspring for breeding.

Comparisons with breeds under stringent economically motivated selection as dairy breeds are not recommendable. Other breeds, where conservation of the population is the top target like the Hinterwald Cattle with 6.5 years (BIEDERMANN *et al.* 2003), exhibit lower values.

Coefficients of coancestry

More than 58% of all White Park Cattle in the German population are related with each other to varying degrees. The maximum value of coancestry amounts to almost 88%.

The observed coefficient of coancestry is higher than those reported for other cattle breeds. Here are examples of coefficients of coancestry in other breeds: Brown Cattle in Baden-Württemberg: 2% (BOLLMEIER *et al.* 1991), Hinterwald Cattle: 2% (BIEDERMANN *et al.* 2003), Vorderwald Cattle: 3.6% (BIEDERMANN *et al.* 2004), German Black Pied Lowland Breed: 4.5% (BIEDERMANN *et al.* 2005).

In all these investigations, population size was typically small and high coefficients of coancestry were expected. Accordingly, ROUGHSEDGE *et al.* (1999) estimated a mean coefficient of coancestry to be only 1.3% in the considerably large population of British Holstein-Friesian. Nevertheless, high mean coefficients of coancestry can be common also in large populations, as it is the case with the population of Holsteins of the United States of America for which YOUNG and SEYKORA (1996) give the tremendously high value of 10.2%. Such populations are characterized by the use of a limited number of sires for artificial insemination.

Inbreeding and main contributors

Due to the possibility of inbreeding depression and increased frequency of recessive homozygotes for deleterious alleles, inbreeding is a great concern.

The mean values of inbreeding found in cattle populations mostly range from 0.3% to 1.7% (HAGGER 1988: Swiss Brown Cattle, MIGLIOR *et al.* 1990, 1995: Canadian Jerseys and Holsteins, BOLLMEIER *et al.* 1991: Brown Cattle of Baden-Württemberg, SCHMIDT 1993: Westphalian Dapple Reds, NAVAJAS and URIOSTE 1995: Aberdeen-Angus of Argentina, YOUNG and SEYKORA 1996: US-American Holsteins, KROGMEIER *et al.* 1997: Gelbvieh and Brown Cattle of South Germany, ROUGHSEDGE *et al.* 1999: British Holstein-Friesians; BIEDERMANN *et al.* 2003: Hinterwald Cattle). Even rather high values of inbreeding estimated for Vorderwald Cattle (2.3%, BIEDERMANN *et al.* 2004), American Holsteins and Jerseys (approximately 5%, CASSEL *et al.* 2000a,b) are less than the coefficient of inbreeding calculated for the White Park Cattle.

Following the statements of JOHANNSON and LUSH (1957), inbreeding does matter if the coefficient of inbreeding exceeds 6.25%. This value, surpassed considerably by the White Parks, shows that they are unparalleled among domestic cattle. Moreover, it has to be considered that historically they have been intensively inbred over many generations. Certainly it can be supposed that the mean inbreeding as well as the mean relationship of them are much higher than indicated by means of only three generations of ancestors. To what extent inbreeding results in depression and threatens a population, is the topic of investigations mostly concerning foreign cattle populations (THOMPSON *et al.* 2000a,b, BIFFANI *et al.* 2002, CARAVIELLO *et al.* 2003, CASSEL *et al.* 2003a,b, UZMAY and AKBAS 2003). It was shown that inbreeding causes depression in all traits which are important for dairy breeding, such as constitution, fertility, and duration of use, which are the traits characterized by a low heritability. But in all these investigations, however, depressions are not of dramatic dimensions in consequence of rather moderate inbreeding. According to the statements of SUJET *et al.* (2001) reproduction traits will be considerably affected only in cases where inbreeding values exceed 12%.

In the literature, the importance of recessive hereditary defects is seldom mentioned. Nevertheless it is important to take them into account. GENTILE *et al.* (2002) report the

frequent occurrence of spastic paresis within the rather small population of Romagnola Cattle in north Italy. They assume that the prevalence of this disease is the result of unavoidably intensive inbreeding.

The key question is, how was the White Park Cattle able to survive up to now without visible defects although they have been intensively inbred over a very long time. Only ALDERSON (2008) mentions that modern White Park Cattle are smaller than their ancient ancestors. This fact is detected by skeletons found in the Chillingham-Park. Certainly it can be expected, that losses of certain alleles caused by inbreeding, have happened during the long history of the breed. Conversely inbreeding can effectively eliminate undesired genes in a population. PIRCHNER (1979) mentions that long periods of inbreeding can lead to resistance against further inbreeding by selectively eliminating deleterious genes. Perhaps White Park Cattle embody an example for such a process.

Finally it is necessary to focus attention on the fact that only a few ancestors in Germany are responsible for the majority of inbreeding within the population. Additionally these ancestors are more or less related to each other, as is documented by their pedigree.

Rate of inbreeding

The effective population size and the rate of inbreeding are of great importance for the future development of a population. They are considered the decisive measures for estimation of the degree of endangerment within a population. High rates of inbreeding and a small effective population size, respectively, are linked to a progressive loss of genetic variability and decrease the potential for future breeding. Concerning the long-term conservation of a population, the German Society of Animal Breeding (Deutsche Gesellschaft für Züchtungskunde, DGfZ) (1992) recommended that the effective size of population N_e should not fall below a value of 50 equivalent to a rate of inbreeding of $\Delta F=1\%$. Nevertheless BREM *et al.* (1990) state that even this value induces an extensive renunciation of selection and successful breeding. In order to realize a successful selection they recommend a minimal effective population size of 100 ($\Delta F=0.5\%$). For the White Park Cattle however, this aspect is not relevant because there is no economic need to improve the breed. In 2004 the Federal Ministry of Consumer Protection, Nourishment and Agriculture (BMVEL) published a »National Program for the Conservation and Enduring Use of Genetic Resources«. In this publication, populations with $N_e\leq0.50$ and $\Delta F\geq1.0\%$, respectively, are termed as »phenotypic populations of conservation«, meaning populations which possess a durable maintenance.

In the light of these recommendations, the German White Park population has to be regarded as highly endangered, because the estimated rate of increase in inbreeding exceeds all above mentioned criteria.

In most cattle populations the rate of inbreeding is significantly lower, for example Murnau-Werdenfels Cattle (GRAML *et al.* 1988), Brown Cattle of Württemberg (BOLLMEIER *et al.* 1991), Westphalian Dapple Reds (SCHMIDT 1993), Canadian Holsteins (MIGLIOR *et al.* 1990, 1995), Gelbvieh and Brown Cattle (KROGMEIER *et al.* 1997), Belgian Blues (HANSET *et al.* 2002), Bavarian Simmentals and Tyrol Grays (PIRCHNER 2002), and Hinterwald and Vorderwald Cattle (BIEDERMANN *et al.* 2002, 2003). Only for the German Black Pied Lowland Breed BIEDERMANN *et al.* (2005) estimated a comparatively high rate of increase of inbreeding of 1.4%, which is still lower than the values found for White Park Cattle.

Conclusions

The average coefficient of coancestry in the investigated German White Park Cattle has been estimated to be 18 % and the average degree of inbreeding to be 16 %. Thus, the White Park Cattle represent a unique phenomenon in the history of animal breeding. The fact that the breed still exists in spite of considerable inbreeding can only be explained by the rigorous natural selection to which it was subjected during all the centuries. Therefore, an extensively stable resistance against inbreeding may have appeared. Nevertheless it seems appropriate to choose breeding animals in a way that minimizes the rate of increase of inbreeding to an unavoidable extent, especially by mating animals related as distantly as possible. For this reason, a careful choice of sires is necessary.

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