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Effect of inbreeding on fertility traits in five dog breeds

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Abstract: The aim of the study was to analyze retrospectively the influence of inbreeding on fertility traits in five dog breeds: German Shepherd dog (GSD), Golden (GR) and Labrador (LR) Retrievers, Beagle and the Tatra Shepherd dog (TSD). The data were 436 litters, with the total of 2560 puppies: 1307 males and 1206 females. The parents of the litters were 163 dogs and 228 bitches. For each litter the litter size, number of male and female puppies, sex ratio, and sex difference were calculated. The fixed effects of breed, of litter birth year and linear regression coefficients on litter and parents' inbreeding were included in the linear model for litter traits. The correlations between litter traits and litter parents' inbreeding were also estimated. The average litter size was 5.87 (± 2.53) for all breeds. GSD had the smallest average litter size differences in years and the lowest fluctuations of sex ratio with litter size. In other dog breeds those differences were much bigger. The difference between the number of male and female offspring in a litter depended on the breed. The lowest percentage of inbred parents was found for LR, and the highest for TSD. Mating non-inbred animals, in most cases also unrelated, was frequent in all breeds. The inbreeding level of parents had significant influence on the litter traits only for TSD. For the Beagles low, positive and significant correlation between the number of female offspring in a litter and the dam's inbreeding level and the sex ratio below 0.5 suggests sex ratio disturbance. The correlation coefficients between litter inbreeding and litter size for majority of examined dog breeds were positive but not significant. The conclusion is that in Poland at first obligatory monitoring of the inbreeding level for all breeds should be applied.

Keywords: dog; reproduction; litter size; sex ratio; inbreeding effect

Several questions related to the increase of inbreeding and its consequences for production, reproduction and health in most of livestock species like cattle, horses, sheep or pigs, have been widely raised, particularly recently. Similar problems, especially concerning genetic health and inbreeding, affect most of purebred dogs, because many dog breeds are limited in size. Recent investigation results indicate that the inbreeding level increase has a negative influence on fertility, health and production of many livestock populations, especially in less popular breeds, and thus little in size, as it has been reviewed by Kania-Gierdziewicz (2013). As Nicolas and Wade (2011) mentioned, purebred dog breeding is a very special branch of animal breeding. In pet animals, like dogs, inbreeding is difficult to avoid because mating between close relatives is still a common practice in many kennels. Additionally, the number of dogs in a breed depends on its popularity and common trends among potential owners or breeders. The size of a dog breed, therefore, is very varied. Only a limited number of dog breeds could be referred to as working dogs. Those populations are usually large and kept in most countries in the world, for example Golden and Labrador Retrievers or German Shepherd dogs. Most of the dog breeds, however, are local ones with a very special kind of use (livestock guarding, hunting, companion or watchdog breeds) and limited in size. Dog breeders in different countries usually have various purposes, hence standardization of breeding programs for a dog breeds and monitoring of their implementation is difficult. On the other

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hand, dog breeding structure is very fragmented. Usually most of the kennels have one, two or three animals, depending on their standards of premises. Few kennels keep more animals, in most cases breeding females, and kennels both with large number of bitches and having additionally sires are scarce, as it is confirmed in Australian research (Shariflou et al. 2011). In addition, formation of modern purebred dog breeds through selective inbreeding of individuals with desired traits (concerning appearance and temperament) frequently leads to bottleneck effects in populations. Therefore, high inbreeding is common in most of pedigree dog populations, and the deterioration in fitness and fertility due to hereditary diseases occurs as well. Recently, the problems with narrowing gene pools of different dog populations caused by inbreeding have been widely investigated (Leroy et al. 2006; Calboli et al. 2008; Oliehoek et al. 2009; Voges and Distl 2009; Maki 2010; Shariflou et al. 2011; Rozanska-Zawieja et al. 2013; Windig and Oldenbroek 2015; Wang et al. 2016).

Stillbirths and hereditary diseases of pupps, or even of entire litters, are currently centrally registered in most countries by national kennel clubs that should supervise the spread of genetic diseases in the populations of various dog breeds in accordance with instructions of FCI (Federation Cynologique Internationale) (Hedhammar et al. 2011; Hedhammar and Indrebo 2011). Loss of heterogeneity and accumulation of detrimental genes in pedigree dog populations, and also the possibilities to alleviate the consequences of those problems, have been pointed out as well (Olafsdottir and Kristjansson 2008; Leroy and Baumung 2010; Windig and Oldenbroek 2015).

The next, now intensively investigated question is that of fertility problems in bitches (lowering of litter size, poor litter viability, stillbirths or cryptorchidism in male pupps) or shortage of male individuals in a litter, and subsequently improper sex ratio and sex difference in a population that could be caused by different environmental and genetic factors, for example inbreeding (Mandigers et al. 1994; Bobic Gavrilovic et al. 2008; Dolf et al. 2008; Gubbels et al. 2009; Borge et al. 2011; Tonnessen et al. 2012; Leroy et al. 2015; Mostert et al. 2015; Sichtar et al. 2016).

The increasing inbreeding level in a dog population could be a cause of not only health or fertility problems, but could also influence the litter size and litter composition (number of male and female puppies), because of early stillbirts of especially male embryos or fetuses. The aim of the work was to perform the retrospective analysis of the influence of inbreeding on litter size, sex ratio, sex difference and on the number of male and female puppies in litters of five dog breeds: German Shepherd dog (GSD), Golden (GR) and Labrador (LR) Retrievers, Beagle and the Tatra Shepherd dog (TSD).

MATERIAL AND METHODS

The study is based on the records of litter data on purebred dogs of five breeds, registered by breeders in the Cracow Branch of Polish Kennel Club (PKC) in the years 2000–2007. Each litter was registered in the PKC at the puppies' age of 6–12 weeks. The PKC data record contained information about parents' IDs and names, the litter birth date and the number of registered male and female puppies. The whole data set kept information about 436 litters, in which totally 2560 puppies (1307 male and 1206 female puppies) were born. As the parents of the examined litters, altogether 163 dogs and 228 bitches were registered. The detailed data set description is given in Table 1.

The distribution of the number of litters and of the number of puppies in the examined time period for the analyzed five breeds is given in Supplementary

Table 1. Detailed description of the data

Item	Breed				
	Beagle	Golden Retriever	Labrador Retriever	Tatra Shepherd dog	German Shepherd dog
Litters *n*	62	65	90	23	196
Total puppies *n*	343	488	585	94	1050
Males	169	264	275	54	545
Females	174	198	289	40	505
Total parents *n*	56	62	92	17	164
Sires	22	21	38	11	71
Dams	34	41	54	6	93

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Figures S1 and S2 in Supplementary Online Material (SOM).

The number of litters registered by sire in each of the five examined dog breeds is given in Supplementary Table S1 in SOM and of those registered by dam in each of five examined dog breeds is given in Supplementary Table S2 in SOM.

The data about the litters were supplemented by the information about inbreeding coefficients of parents estimated earlier (Gierdziewicz et al. 2011; Kania-Gierdziewicz et al. 2011, 2014, 2015). Based on the relationship coefficients of each pair of parents, the inbreeding coefficients of pupps in each litter were assessed. The average inbreeding coefficient values for all parents, for sires and for dams were estimated for each breed. For the evaluation of pedigree completeness the mean equivalent of complete generations (EqG) was estimated according to Boichard et al. (1997) as follows:

$$\text{EqG} = \frac{1}{N}\sum_{j=1}^{N}\sum_{i=1}^{n_j}\frac{1}{2^{g_{ij}}}$$

where:

EqG = mean equivalent of complete generations

N = number of examined animals

n_i = total number of ancestors of animal j in the population under study

g_{ij} = number of generations between animal j and its ancestor i

Also, for each breed the number of litters of sires and dams inbred (i.e. whose parents were related) and non-inbred (i.e. whose parents were unrelated), including the information about the mating structure concerning the inbreeding coefficients values of parents were investigated. The relationship coefficients of each pair of parents were also analyzed. The mating structure is usually as follows: both parents could be non-inbred ($R_{XY} = 0$ between sire and dam of each parent) or inbred ($R_{XY} > 0$ between sire and dam of each parent) or only one of them could be inbred, and at the same time parents could be unrelated ($R_{XY} = 0$ between sire and dam) or related ($R_{XY} > 0$ between sire and dam).

For each litter from the analyzed five dog breeds the following traits were calculated: litter size (LS), the number of male (NM) and female (NF) puppies per litter, sex ratio (SR) within a litter as the number of male offspring divided by the number of all offspring in a litter, and sex difference (RN), which is the difference between number of males and females in a litter (Dolf et al. 2008). The average SR should normally have the value over 0.5 indicating that in a balanced population more males than females are born, because of higher mortality of male offspring. RN is positive if there are more male than female offspring in a litter, zero if the numbers of male and female offspring are equal and negative otherwise.

The first linear model of all the analyzed traits was as follows: the fixed effects of breed and litter birth year, and also the interaction between these effects, were included in the 2-way linear model definition for the analysis of variance performed by using GLM procedure of SAS/STAT (Version 13.2, 2014) for litter traits. The effect of the interaction between litter birth year and breed was not significant ($P > 0.05$) and therefore it was not included in the subsequent analysis. Litter birth year effect was also not significant for all traits except NM, for which it was significant ($P < 0.05$, $R^2 = 0.145$). The breed effect, however, was highly significant ($P < 0.01$) for LS ($R^2 = 0.166$), number of male puppies ($R^2 = 0.145$) and number of female puppies ($R^2 = 0.108$). For SR the breed effect was only significant ($P < 0.05$, $R^2 = 0.106$) and for sex difference it was not significant ($P > 0.05$, $R^2 = 0.089$).

In the next analysis the effects of the parents' inbreeding levels on the examined progeny traits were estimated with two linear models referred to as Model 1 and Model 2. The fixed breed effect for all traits and the litter birth year effect (for the number of male offspring) and also linear regression coefficients on the inbreeding effect of parents were included in both models.

Model 1 of LS, NF, SR and RN for an animal of $i^{\text{-th}}$ breed with parents j and k was as follows:

$$y_{ijkl} = \mu + \text{breed}_i + b_1(\text{Fs}_j - \text{Fs}) + b_2(\text{Fd}_k - \text{Fd}) + e_{ijkl} \quad (1)$$

where:

y_{ijkl} = value of a trait (LS, NF, SR or RN)

μ = overall mean

breed_i = fixed effect of $i^{\text{-th}}$ breed ($i = 1, ..., 5$)

b_1 = linear regression on sire inbreeding coefficient

Fs_j = $j^{\text{-th}}$ sire inbreeding coefficient

Fs = mean inbreeding coefficient of sires

b_2 = linear regression on dam inbreeding coefficient

Fd_k = $k^{\text{-th}}$ dam inbreeding coefficient

Fd = mean inbreeding coefficient of dams

e_{ijkl} = random residual

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Model 2 of NM for an animal of $i^{\text{-th}}$ breed born in $j^{\text{-th}}$ birth year with parents k and l was:

$$y_{ijklm} = \mu + \text{breed}_i + \text{year}_j + b_1(\text{Fs}_k - \text{Fs}) + b_2(\text{Fd}_l - \text{Fd}) + e_{ijklm} \quad (2)$$

where:

y_{ijklm} = value of a trait (NM)

year_j = fixed $j^{\text{-th}}$ litter birth year effect (j = 2,..., 8)

μ, breed_i, b_1, b_2, Fs_k, Fd_l, Fs, Fd and e_{ijklm} – as described above

The subsequent analysis concerned the influence of the litter inbreeding level on the examined litter traits. Again, two linear models were used: Model 3 for all traits except the number of male offspring and Model 4 for the NM trait. The fixed breed effect for all traits and for NM, the litter birth year effect, and linear regression coefficients on the litter inbreeding effect were included in both models. The following Model 3 for LS, NF, SR and RN was used:

$$y_{ijk} = \mu + \text{breed}_i + b_3(\text{Flit}_j - \text{Flit}) + e_{ijk} \quad (3)$$

where:

y_{ijk} = value of a trait (LS, NF, SR or RN)

μ = overall mean

breed_i = fixed effect of $i^{\text{-th}}$ breed (i = 1,..., 5)

b_3 = linear regression on litter inbreeding coefficient

Flit_j = $j^{\text{-th}}$ litter inbreeding coefficient

Flit = mean inbreeding coefficient of litters

e_{ijk} = random residual

For NM, the Model 4 was as follows:

$$y_{ijkl} = \mu + \text{breed}_i + \text{year}_j + b_3(\text{Flit}_k - \text{Flit}) + e_{ijkl} \quad (4)$$

where:

y_{ijkl} = value of a trait (NM)

year_j = fixed $j^{\text{-th}}$ litter birth year effect (j = 1,..., 8)

μ, breed_i, b_3, Flit_k, Flit and e_{ijkl} – as described above

Due to highly significant breed effect on the litter traits, Spearman correlation coefficients (SAS/STAT, Version 13.2, 2014) between fertility traits and sire or dam inbreeding effects or between fertility traits and litter inbreeding effect for each breed were estimated as well.

RESULTS AND DISCUSSION

The number of litters and the number of puppies registered in each year in the five analyzed dog breeds increased step by step in time for all breeds except TSD and German Shepherds. In TSD the number of litters and puppies registered were, in general, low. In some years single litters with only one puppy were registered. Meanwhile, in GSD, constantly the most popular breed in Poland, the numbers of litters and puppies registered by year were almost fixed, reaching about 20–25 litters/year and from 100 to over 140 puppies per year. The exceptions were 37 litters with over 180 puppies registered in 2001 and only 13 litters with a little over 60 puppies registered in 2004 (Supplementary Figures S1 and S2 in SOM).

Most of sires in each of the five examined dog breeds became the fathers of one litter, only a few sires had left two or more litters. The only exception was GSD breed with 16 sires having two registered litters each. A larger number of litters per sire, meaning that the sire was used more intensively or for a longer time than others, was a rarity in the analyzed dog breeds (Supplementary Table S1 in SOM). Usually there were only single distinguished sires of that kind, for example one of the GR sires became the father of 20 litters. In Beagle and GSD breeds there were two sires in each breed that left 13 and 15 litters, respectively.

Similarly, most dams left only one or two litters. The exception were the German Shepherd dams, which often became the mothers of third litter as well. Generally speaking, the reproductive life of a bitch in most of the examined breeds ended up after the third, fourth or, like in GSD, fifth whelping. Bitches with longer reproductive use were scarce; there were only two such dams: one Beagle dam with 8 litters and also one German Shepherd dam with 7 litters (Supplementary Table S2 in SOM).

The mean LS and also the minimum and maximum values of LS for the five dog breeds are given in Table 2. The highest single LS values were found in GR (maximally 13 puppies) and in GSD (maximally 12 puppies), and the Beagle breed had the lowest maximum LS (10 puppies). The highest average LS (over 7.5 heads) was found in GR breed; the lowest, reaching about 4 puppies, was that of the TSD breed. This was confirmed by the GLM analysis: the breed effect was highly significant for all examined breeds. Most of the examined dog breeds showed the appropriate SR values, which exceeded 0.5, except Beagles and LR breed for which the value was lower than 0.5. The GLM analysis showed that the SR value for LR was

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Table 2. Basic statistical measures of litter size, number of male and female puppies, sex ratio and sex difference for five dog breeds

Item	Breed				
	Beagle	Golden Retriever	Labrador Retriever	Tatra Shepherd dog	German Shepherd dog
Litters *n*	62	65	90	23	196
Litter size					
Mean	5.53	7.51	6.50	4.09	5.36
SD	1.91	2.46	2.19	3.54	2.40
Range	2–10	1–13	2–11	1–11	1–12
Male puppies *n*					
Mean	2.73	4.26	3.16	3.13	2.80
SD	1.51	1.85	1.92	2.29	1.68
Range	0–7	1–9	0–8	0–8	0–9
Female puppies *n*					
Mean	2.81	3.19	3.30	2.13	2.58
SD	1.45	1.65	1.62	1.64	1.67
Range	0–8	0–8	0–8	0–5	0–7
Sex ratio					
Mean	0.48	0.58	0.47	0.57	0.52
SD	0.22	0.18	0.25	0.38	0.27
Sex difference					
Mean	–0.08	1.06	–0.16	0.61	0.20
SD	2.25	2.48	2.77	1.75	2.34

significantly lower but for GR it was significantly higher than for other breeds. RN values were positive and above zero. The exceptions were found in Beagle and LR breeds. Both breeds showed SR values lower than 0.5 and negative RN values, which indicates a shortage of male progeny in those two breeds (also shown by NM and NF mean values). The GLM analysis revealed that significant differences in NM existed for all breeds and in NF they were found for all breeds except Beagle. In RN the significant differences were found only for both retriever breeds (Table 2). The effect of birth year of litter in Model 2 and Model 4 for the number of males in the litter was not significant ($P > 0.05$) if it was used with the effect of parents or litter inbreeding as regression coefficients.

Many environmental and genetic factors affect more or less LS and other fertility traits in dogs, but the most important genetic factors are the size of dog breed, its genetic structure and inbreeding level. Borge et al. (2011) found the same mean LS values as in our study for Beagle and GR breeds registered in the Norwegian Kennel Club. However, average LS for LR and GSD breeds was lower than that reported by the cited authors. The maximum LSs for all examined dog breeds, except Beagle, were lower in our study than for GR and GSD and for LR, while for the Beagle breed our result for maximum LS was in accordance with the findings in the aforementioned paper. Leroy et al. (2015) for GSD obtained a little bit lower mean LS than in our study. For 5412 GR puppies from 840 litters Nielen et al. (2001) estimated lower value of LS (6.44) than in our study. For South African Boxers, Mostert et al. (2015) found average LS of 6.14 (± 2.43) with maximum LS of 14 puppies which was higher than in the majority of breeds in our study, except both Retriever breeds. In GSD used by Police of the Czech Republic, Sichtar et al. (2016) estimated mean LS value as 6.9 (± 3.1) and maximum LS reaching 14, which was significantly higher than in the present study for the same dog breed. The mean LS for Beagle, Golden and Labrador Retrievers provided by Tonnessen et al. (2012) were lower than in our study, but the corresponding value for German Shepherds was higher than ours.

The average LSs in the analyzed time period for the five dog breeds are given in Figure 1. The average LS of 5.87 (± 2.53) puppies per litter was

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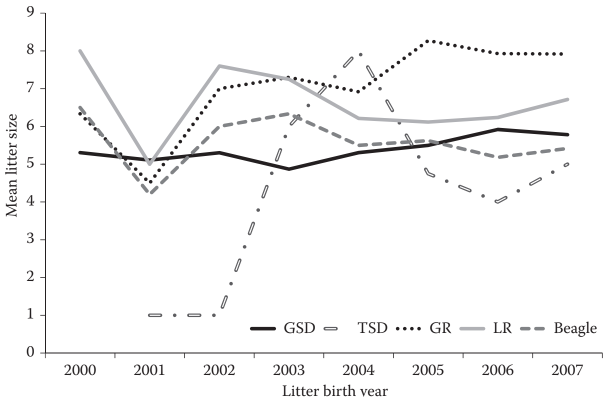

Figure 1. Distribution of the mean litter size by birth year in five dog breeds

GSD = German Shepherd dog, TSD = Tatra Shepherd dog, GR = Golden Retriever, LR = Labrador Retriever

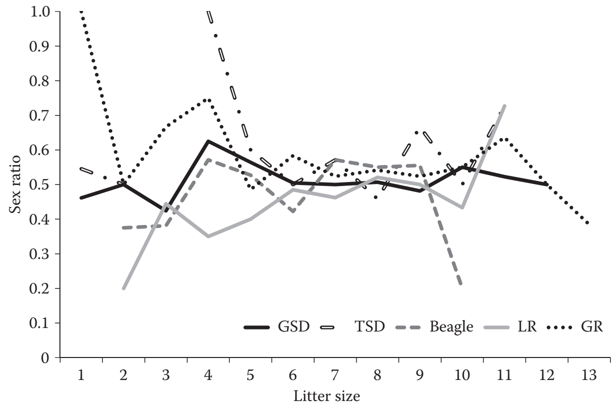

Figure 2. Sex ratio for different litter sizes in five dog breeds

GSD = German Shepherd dog, TSD = Tatra Shepherd dog, GR = Golden Retriever, LR = Labrador Retriever

estimated for all breeds. GSD had the smallest average LS differences in years. In other dog breeds the differences in LS were much bigger, especially in the years 2000–2003. Vast majority of the differences in LS can be noticed in TSD because of the small number of litters registered every year (Figure 1).

The number of litters of different size for the five dog breeds is given in Supplementary Figure S3 in SOM. In both Retriever breeds most of the litters numbered 8 (LR) and 9 puppies (GR). The Beagle and GSD breeds had most of the litters with 6 puppies and the TSD with only one puppy (Supplementary Figure S3 in SOM.).

In Figure 2 the SR distribution over LS is shown for all the examined dog breeds. SR in litters with 5–9 puppies for all analyzed breeds (Figure 2) oscillated around the value 0.5 which refers to the proportion of 1 : 1. The litters with lower size (1–5 puppies) in GR and TSD numbered more male offspring and in LR more female. Similarly, in the litters with more than 9 puppies of the Beagle and GR breeds the female offspring were superior in numbers. The GSD revealed the lowest fluctuations of SR depending on LS increase (Figure 2). However the significant differences in average SR have occurred only for GR and LR breeds (Table 2).

Gubbels et al. (2009) analyzed 11 230 litters from 12 dog breeds with the different mating pattern of cryptorchidism "carrier" and "non-carrier" parents. They found that for eight breeds (Beagle, Border Terriers, German Boxers, Cairn Terriers, Drentse Partrige Dogs, German Hounds, Flat-coated Retrievers and Scottish Sheepdogs) males outnumbered females in the litter if the parents were "non-carriers". Only for four dog breeds (Chow Chows, Schapendoes, Shetland Sheepdogs and West Highland White Terriers) predominance of female puppies in a litter was found (Gubbels et al. 2009). The overall average SR for the 12 dog breeds was calculated by the above mentioned authors as 101.6 males per 100 females and for "non-carrier" parents – 101.2 males per 100 females. Also, Mostert et al. (2015) for South African Boxers found that, on the average, more male than female puppies in a litter were born (3.23 vs 2.91, respectively).

Figure 3 shows sex difference (RN) for different LS in five dog breeds examined. The difference between the number of male and female offspring in a litter (RN) depended on breed. For LR in most cases the RN values were negative, which means that in litters of almost all the sizes there were more female offspring, with two exceptions: the litters with sizes of 8 and 11, in which there were more male than female puppies. In the Beagle breed, only in the litters sizing 7–9 puppies there were more males than females. The TSD showed male superiority in numbers for LSs up to 5 puppies and also for larger litters (7–11 puppies). Meanwhile, for the GR breed the RN values were positive or equal to zero, i.e. the number of male and female offspring was equal or there were more males than females in a litter, except the largest litters (13 puppies) in which there were more female offspring. The RN values for most LSs in GSD were equal to zero, except the litters with 4–5

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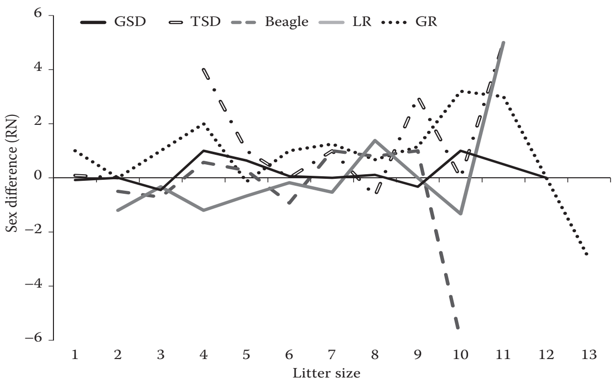

Figure 3. Sex difference (RN) for different litter sizes in five dog breeds

GSD = German Shepherd dog, TSD = Tatra Shepherd dog, GR = Golden Retriever, LR = Labrador Retriever

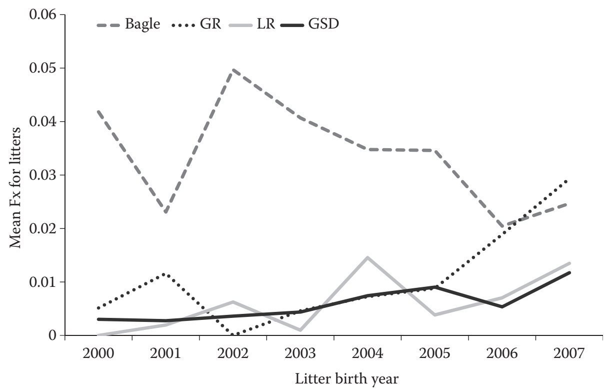

Figure 4. Mean litter Fx coefficients distribution by birth year

GSD = German Shepherd dog, GR = Golden Retriever, LR = Labrador Retriever

and 10–11 puppies, in which more male offspring were born (Figure 3).

The lowest percentage of inbred parents (ca. 7.6%) was found in the LR breed, and the highest in the TSD breed where over half the parents (52.9%) were inbred. For other dog breeds the percentages were also high and reached 44.6%, 31.7% and 25.8% for Beagle, GSD and GR, respectively. In the TSD and Beagle breeds the highest average F_x values for parents were estimated. The parents from the remaining three breeds were less inbred.

The mean EqG values were 3.5 for TSD, 6 for Beagle, LR and GSD and 6.3 for GR. In Tables 3 and 4 the inbreeding coefficients of sires and dams, respectively, of the litters from the analyzed dog breeds are shown.

The lowest percentages of inbred sires and dams were found in the LR breed, reaching 7.9% and 7.4% for sires and dams, respectively. On the other hand, the highest inbred animals percentage was calculated for TSD – about 54.6% and 50% for sires and dams, respectively. The remaining dog breeds revealed more inbred dams than sires. The corresponding percentage values for sires were 31.8%, 19% and 28.2% and for dams 52.9%, 29.3% and 34.4% for Beagle, GR and GSD, respectively. The highest mean F_x values in sires and dams

Table 3. Total number of sires, number of inbred sires and mean inbreeding coefficient (F_x) values for all and inbred sires

Item	Breed				
	Beagle	Golden Retriever	Labrador Retriever	Tatra Shepherd dog	German Shepherd dog
Total sires *n*	22	21	38	11	71
Inbred sires *n*	7	4	3	6	20
Mean F_x (all sires)	0.0212	0.0041	0.0027	0.0322	0.0059
Mean F_x (inbred sires)	0.0667	0.0215	0.0337	0.0591	0.0211
Maximum F_x of sire	0.1016	0.0391	0.0700	0.1406	0.1055

Table 4. Total number of dams, number of inbred dams and mean inbreeding coefficient (F_x) values for all and inbred dams

Item	Breed				
	Beagle	Golden Retriever	Labrador Retriever	Tatra Shepherd dog	German Shepherd dog
Total dams *n*	34	41	54	6	93
Inbred dams *n*	18	12	4	3	32
Mean F_x (all dams)	0.0258	0.0043	0.0051	0.0339	0.0052
Mean F_x (inbred dams)	0.0488	0.0148	0.0688	0.0677	0.0150
Maximum F_x of dam	0.1328	0.0469	0.1250	0.1016	0.0644

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Table 5. Number (*n*) and percentage (%) of different mating patterns by inbreeding and kinship of parents

Mating pattern	Breed									
	Beagle		Golden Retriever		Labrador Retriever		Tatra Shepherd dog		German Shepherd dog	
	n	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)
Both parents non-inbred	17	27.4	39	60.0	73	83.0	7	46.70	64	33.2
Only sire inbred	9	14.5	8	12.3	9	10.2	3	20.00	51	26.4
Only dam inbred	25	40.3	13	20.0	4	5.0	1	7.00	40	20.7
Both parents inbred	11	17.7	5	7.7	2	2.3	4	26.70	38	19.7
Related parents	40	64.5	44	67.7	35	39.8	4	0.27	72	37.3
Unrelated parents	22	35.5	21	32.3	53	60.2	11	0.73	121	62.7
Related non-inbred parents	12	19.4	25	38.5	25	28.4	0	0.00	4	0.02
Related inbred parents	9	14.5	5	7.7	2	2.3	4	0.27	36	18.7
Related, one parent inbred	19	30.6	14	21.5	8	9.1	0	0.00	32	16.6
Unrelated non-inbred parents	5	8.1	14	21.5	48	54.5	7	0.47	59	30.6
Unrelated inbred parents	2	3.2	0	0.0	0	0.0	0	0.00	2	0.01
Unrelated, one parent inbred	15	24.2	7	10.8	5	5.7	4	0.27	60	31.1

were estimated for Beagle and TSD; the dams of both breeds were more inbred than the sires. The maximum F_x values exceeding 0.1 were found both in dams and sires from Beagle and TSD breeds, and also for LR dams and GSD sires (Tables 3–4).

In most of the investigated dog breeds non-inbred sires were used much more intensively than the inbred ones. The exception was TSD with more inbred individuals used for reproduction. Also, in the GSD breed inbred sires were longer used for reproduction and they left more litters per sire than non-inbred sires. The non-inbred dams also left much more litters than inbred ones, with two exceptions: in the Beagle breed there were in total more whelpings of inbred than of non-inbred dams and in the GSD breed the inbred and non-inbred bitches left almost the same number of litters. Also the dams of both breeds mentioned above, with 7 or 8 litters, were inbred.

The distribution of mean inbreeding coefficients for litters according to litter birth year for dog breeds, except TSD, is given in Figure 4. TSD were not included because in this breed only three inbred litters occurred in two years of the examined time period. The steady little increase of the mean inbreeding values was found for all examined breeds except Beagles, for which the average F_x coefficients after 2002 year were decreasing.

The numbers of different matings by inbreeding pattern and kinship of parents for the five dog breeds are given in Table 5. Mating pattern analysis (Table 5) shows that mating non-inbred animals was frequent in all breeds except the Beagles, in which non-inbred sires were more often mated to inbred dams. In the GSD breed, on the other hand, also inbred sires were often mated to non-inbred dams. In both breeds mentioned above and also in TSD mating the inbred animals was frequent. Meanwhile, in both Retriever breeds those patterns of mating were rarely used (Table 5). In general, the breeders of all investigated dog breeds tried to avoid mating inbred animals, whenever possible. It could be, obviously, much easier for the most popular and large breeds, like Retrievers or German Shepherds. However, for less popular dog breeds it could be possible as well, but more demanding, requiring more involvement from the breeders' part.

In the Beagle and GR breeds most (over 67%) parents were related and most of them were non-inbred whereas for other examined dog breeds matings between unrelated parents were most

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Table 6. Estimated correlation coefficients between sire's or dam's inbreeding level (F_x) and litter size (LS), number of male offspring in a litter (NM), number of female offspring in a litter (NF), sex ratio (SR) and sex difference (RN) for all dog breeds

Traits	Breed									
	Beagle		Golden Retriever		Labrador Retriever		Tatra Shepherd dog		German Shepherd dog	
	sire F_x	dam F_x	sire F_x	dam F_x	sire F_x	dam F_x	sire F_x	dam F_x	sire F_x	dam F_x
LS	0.12	0.23	0.01	–0.18	0.04	0.02	–0.34	0.83***	–0.07	–0.05
NM	–0.05	0.04	–0.09	–0.08	0.12	0.04	–0.37	0.78**	0.03	0.02
NF	0.20	0.27*	0.11	–0.20	–0.08	–0.04	–0.21	0.62*	–0.14	–0.10
SR	–0.13	0.09	–0.25	0.18	0.04	0.08	–0.64*	–0.16	0.16*	0.11
RN	–0.16	–0.15	–0.15	0.08	0.13	0.05	–0.27	0.28	0.12	0.09

coefficients significant at *P < 0.05, **P < 0.01, ***P < 0.001

frequent. In both Retriever breeds in most cases the mated parents were non-inbred, no matter how closely they were related. On the other hand, in mating Beagle parents – related or not – one of them was frequently inbred. In GSD, mating related and inbred parents, and also mating unrelated animals if one of them was inbred, was frequent (Table 5).

Calboli et al. (2008) examined the population structure and inbreeding in 10 dog breeds from the UK and found F_x values ranging from over 0.033 to more than 0.073, which is slightly higher than our results. They also found much higher maximum inbreeding coefficients for GR (0.39), GSD (0.47) and LR (0.39), which indicated that mating closely related animals was more frequent than in our study. Also Wang et al. (2016) found that for French, Swedish and UK populations of four dog breeds the breeders very often mated related animals, but with downward tendency. For LR they found that the frequency of mating related animals was low and quite stable in all countries examined which is in accordance with our results.

Leroy et al. (2015) investigated the influence of inbreeding on LS and longevity for seven dog breeds, among others for German Shepherds. They found that the inbreeding coefficients for the litters ranged from 0.02 up to slightly over 0.05, and about 75–90% of all litters showed low inbreeding level (F_x < 0.0625) and only 3.5–8% litters had high inbreeding coefficients (F_x ≥ 0.125). For GSD, Leroy et al. (2015) obtained F_x = 0.024, 88% litters in low inbreeding class and 3.6% litters in high inbreeding class, which means that mating close relatives was not popular for this dog breed in France. Mostert et al. (2015) found that about 28% of examined South African Boxers were not inbred, in most cases because of lack of pedigree information and about 72% dogs were inbred, which was much higher than in our results, and which means that mating close relatives was a common practice in Boxer population. Over 28% Boxer dogs had inbreeding coefficients between 0.0625 and 0.125. About 16.7% animals had F_x greater than 0.125. The highest inbreeding coefficient value in South African Boxer population reached 0.427 for four animals (two males and two females) from one litter. The authors stated that Boxer breeders participated in recording pedigrees and fitness traits, which could be positive and should help monitor inbreeding levels, rate of inbreeding and the effect of inbreeding on fertility and fitness traits and recommended reducing the inbreeding level, which has recently increased in Boxer population by 0.14% per year (Mostert et al. 2015).

The analysis of variance results showed that inbreeding level of parents had no significant influence (P > 0.05) on the litter traits, because the number of inbred sires or dams was in general low in all examined breeds (see Tables 3–4). Besides, the inbreeding coefficient values for parents were rather low. The F_x values over 0.0625, which could cause health and fertility problems (Leroy et al. 2015), were found only for individual animals in parental group of each breed. Therefore the analysis should be continued with the use of more inbred animals. The correlation coefficients estimated between parents inbreeding level and litter traits are showed in Table 6.

Most values of Spearman correlation coefficient between the inbreeding level of sires and dams and the LS assessed for five dog breeds were low

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Table 7. Correlation coefficients estimated between litter inbreeding level (F_x) and litter size (LS), number of male offspring in a litter (NM), number of female offspring in a litter (NF), sex ratio (SR) and sex difference (RN) for all dog breeds

Traits	Beagle		Golden Retriever		Labrador Retriever		Tatra Shepherd dog		German Shepherd dog	
	litter F_x	Pr >|r|	litter F_x	Pr >|r|	litter F_x	Pr >|r|	litter F_x	Pr >|r|	litter F_x	Pr >|r|
LS	–0.006	0.9641	–0.095	0.4509	0.025	0.8166	0.469	0.0777	0.149*	0.0381
NM	–0.030	0.8145	0.136	0.2936	0.109	0.3194	0.368	0.1762	0.093	0.1990
NF	0.023	0.8535	0.009	0.9464	–0.087	0.4250	0.488	0.0645	0.121	0.0929
SR	–0.008	0.9481	0.061	0.6361	0.132	0.2261	–0.038	0.8944	–0.052	0.4726
RN	–0.036	0.7826	0.096	0.4591	0.126	0.2477	0.023	0.9345	–0.020	0.7844

Pr = probability; coefficients significant at *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

(positive or negative) and even near zero, but almost all for four out of examined breeds were non-significant. On the other hand, correlation coefficient between LS and inbreeding level for TSD dams had high, positive value and was significant, which means that with increasing dam's inbreeding level the LS in the TSD was growing up as well. Similarly, for the TSD breed the correlations between NM or NF and the dam's inbreeding level had significant, high and positive values (Table 6).

The number of inbred litters was different among the examined breeds. The higher percentage, reaching 67.7% of inbred litters, was found in the Beagle and GR breeds. In LR and GSD there were 40% and 36.7% inbred litters, respectively. In TSD only 17% of litters were inbred, but the average inbreeding coefficient value for this breed was the highest, reaching 0.083. The mean F_x values for the litters of the other breeds were: 0.041, 0.025, 0.017 and 0.014 for Beagle, LR, GR and GSD, respectively. The effect of litter inbreeding level on the litter traits was statistically not significant ($P > 0.05$), because in most breeds there were only a few highly inbred litters ($F_x > 0.0625$). The issue presented in this paper needs more investigation especially with the use of more litters with high inbreeding levels.

Spearman correlation coefficients between the litter inbreeding level and the litter traits are shown in Table 7. The correlation coefficients between litter inbreeding and LS for the majority of the examined dog breeds were positive, with medium or low values, and not significant. Significant values were also found for the correlation coefficients between the litter inbreeding and the LS for GSD or the number of female puppies in litter and the litter inbreeding for TSD (near to significance). All these correlations were positive and showed a little positive relationship between the litter inbreeding and the above mentioned traits for these breed (Table 7).

Mandigers et al. (1994) found a negative influence of homozygosity of puppies on LS. The authors concluded that LS depends on many factors (genetic and environmental). The above mentioned authors found also that the LS increased with decreasing of the parents' inbreeding values. Mostert et al. (2015) found also that for every 1% increase of inbreeding, the LS of the South African Boxers decreased by 0.85 puppy.

Leroy et al. (2015) obtained the results for the negative impact of inbreeding on LS for seven dog breeds in France. They found that for all those dog breeds the LS was significantly reduced when the litter was inbred, in contrast to our findings for some dog breeds. High inbreeding of the dam had the same effect on LS according to Leroy et al. (2015) (for German Shepherd females). Our results for GSD dams were similar but not significant. Also Urfer (2009) found a highly significant, although low influence of the dam's inbreeding level on LS in Irish Wolfhounds in Sweden.

The effect of the parents inbreeding level on fertility traits (LS, NM, NF, SR and RN) was not significant. In the case of Beagles, positive and significant correlation of NF with the inbreeding of the dam indicates that the latter rose with the former. Likewise, the positive and significant correlation of SR with sire inbreeding in GSD suggests that the increase of the latter shifted the sex ratio towards a greater number of male puppies in the litter, which is, in that case, advantageous. In the both aforementioned breeds only about 30% matings were those with two inbred parents. In both retriever breeds no effect

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of parent inbreeding on the examined traits was detected; the estimated correlation coefficients were low or near zero and therefore, naturally, insignificant, though in LR an undesirable lowering of the number of males was noticed. Probably that state of affairs is due rather to non-genetic factors. In TSD the significant influence of dam inbreeding on LS, NM and NF as well as the negative correlation of sire inbreeding with SR, was found, which may indicate that inbred dams improved the sizes of their litter whereas inbred sires definitely deteriorated the proportion of sexes, resulting in more female puppies; that is in agreement with the literature findings mentioned before. However, since the studied breed has a local character and has a relatively small number of parents and, consequently, whelpings, the results are to be treated only as approximate. The effect of litter inbreeding on the examined traits (LS, NM, NF, SR, RN) was not found in our study. The corresponding correlation coefficients between the inbreeding level of the litter and those traits were very low and insignificant, except the low positive correlation of the litter inbreeding level with its size in GSD, which could suggest that the inbred litters had a slightly greater size. The dog breeds that were examined in this paper differ in popularity and, consequently, in size, which is also associated with the mating pattern. As it has been shown in various studies, in more popular breeds (like retrievers or GSD) there is a greater possibility to avoid mating related individuals and therefore controlling the increase of inbreeding level is easier. In less sized breeds, like Beagles or, in particular, TSD it is rather difficult. Nevertheless, the FCI regulations concerning monitoring the frequency of genetic disorders, the law already introduced in many countries, should also be taken into account in Poland, and especially the breeds with detected increase in the number of females in the progeny of inbred parents should be monitored. This would require the obligatory monitoring of such breeds for a possible increase of inbreeding level.

CONCLUSION

In most of the investigated dog breeds non-inbred sires or dams were used much more intensively than the inbred ones. Therefore the breeders of all investigated dog breeds tried to avoid mating inbred animals, whenever possible.

The influence of the parents inbreeding level on fertility traits was not significant in most of the dog breeds examined. The effect of litter inbreeding on the examined fertility traits was not found in our study. Because of the little number of highly inbred sires, dams or litters found in this study, the problem presented in this paper needs more investigation.

The authors also suggest to introduce obligatory monitoring of the inbreeding level for all dog breeds in Poland, especially for those less popular and thus less numerous.

REFERENCES

Bobic Gavrilovic B., Andersson K., Linde Forsberg C. (2008): Reproductive patterns in the domestic dog – A retrospective study of Drever breed. Theriogenology, 70, 783–794.

Boichard D., Maignel L., Verrier E. (1997): The value of using probabilities of gene origin to measure genetic variability in a population. Genetics Selection Evolution, 29, 5–23.

Borge K.S., Tonnessen R., Nodtvedt A., Indrebo A. (2011): Litter size at birth in purebred dogs – A retrospective study of 224 breeds. Theriogenology, 75, 911–919.

Calboli F.C.F., Sampson J., Fretwell N., Balding D.J. (2008): Population structure and inbreeding from pedigree analysis of purebred dogs. Genetics, 179, 593–601.

Dolf G., Gaillard C., Schelling C., Hofer A., Leighton E. (2008): Cryptorchidism and sex ratio are associated in dogs and pigs. Journal of Animal Science, 86, 2480–2485.

Gierdziewicz M., Kania-Gierdziewicz J., Kalinowska B. (2011): Analysis of genetic structure of the Beagle population in the area of Cracow Branch of the Polish Kennel Club. Animal Science Papers and Reports, 29, 359–367.

Gubbels E.J., Scholten J., Janss L., Rothuizen J. (2009): Relationship of cryptorchidism with sex ratios and litter sizes in 12 dog breeds. Animal Reproduction Science, 113, 187–195.

Hedhammar A., Indrebo A. (2011): Rules, regulations, strategies and activities within the Fédération Cynologique Internationale (FCI) to promote canine genetic health. The Veterinary Journal, 189, 141–146.

Hedhammar A., Malm S., Bonnett B. (2011): International and collaborative strategies to enhance genetic health in purebred dogs. The Veterinary Journal, 189, 189–196.

Kania-Gierdziewicz J. (2013): Analysis of population genetic structure as a tool to preserve genetic resources – a review. Wiadomości Zootechniczne, 51, 107–120. (in Polish)

https://doi.org/10.17221/104/2017-CJAS

Kania-Gierdziewicz J., Kalinowska B., Gierdziewicz M. (2011): Inbreeding and relationship in the German Shepherd dog population in area of Cracow Branch of Polish Kennel Club. Scientific Annals of Polish Society of Animal Production, 7, 21–29.

Kania-Gierdziewicz J., Gierdziewicz M., Kalinowska B. (2014): Inbreeding and relationship analysis of the Golden and Labrador Retriever populations in the Cracow Branch of the Polish Kennel Club. Scientific Annals of Polish Society of Animal Production, 10, 9–19. (in Polish)

Kania-Gierdziewicz J., Gierdziewicz M., Budzynski B. (2015): Genetic structure analysis of Tatra Shepherd dog population from Tatra Mountain region. Annals of Animal Science, 15, 323–335.

Leroy G., Baumung R. (2010): Mating practices and the dissemination of genetic disorders in domestic animals, based on the example of dog breeding. Animal Genetics, 42, 66–74.

Leroy G., Rognon X., Varlet A., Joffrin C., Verrier E. (2006): Genetic variability in French dog breeds assessed by pedigree data. Journal of Animal Breeding and Genetics, 123, 1–9.

Leroy G., Phocas F., Hedan B., Verrier E., Rognon X. (2015): Inbreeding impact on litter size and survival in selected canine breeds. The Veterinary Journal, 203, 74–78.

Maki K. (2010): Population structure and genetic diversity of worldwide Nova Scotia Duck Tolling Retriever and Lancashire Heeler dog populations. Journal of Animal Breeding and Genetics, 127, 318–326.

Mandigers P.J.J., Ubbink G.J., Van den Broek J., Bouw J. (1994): Relationship between litter size and other reproductive traits in the Dutch Kooiker dog. Veterinary Quarterly, 16, 229–232.

Mostert B.E., van Marle-Koster E., Visser C., Oosthuizen M. (2015): Genetic analysis of pre-weaning survival and inbreeding in the Boxer dog breed of South Africa. South African Journal of Animal Science, 45, 476–484.

Nicolas F.W., Wade C.M. (2011): Canine genetics: A very special issue. The Veterinary Journal, 189, 123–125.

Nielen A.L.J., van der Beek S., Ubbink G.J., Knol B.W. (2001): Epidemiology: Population parameters to compare dog breeds: Differences between five Dutch purebred populations. Veterinary Quarterly, 23, 43–49.

Olafsdottir G.A., Kristjansson T. (2008): Correlated pedigree and molecular estimates of inbreeding and their ability to detect inbreeding depression in the Icelandic sheepdog, a recently bottlenecked population of domestic dogs. Conservation Genetics, 9, 1639–1641.

Oliehoek P.A., Bijma P., van der Meijden A. (2009): History and structure of the closed pedigreed population of Icelandic Sheepdogs. Genetics Selection Evolution, 41, 39–51.

Rozanska-Zawieja J., Nienartowicz-Zdrojewska A., Mucha M., Sobek Z., Stanislawski D., Gierdziewicz M., Kania-Gierdziewicz J. (2013): Evaluation of inbreeding and relationship coefficients in Hovawart dogs and analysis of trends in coat colour changes. Annals of Animal Science, 13, 253–262.

Sichtar J., Dokoupilova A., Vostry L., Rajmon R., Jilek F. (2016): Factors affecting reproductive efficiency in German Shepherd bitches producing litters for Police of the Czech Republic. Czech Journal of Animal Science, 61, 578–585.

Shariflou M.R., James J.W., Nicolas F.W., Wade C.M. (2011): A genealogical survey of Australian registered dog breeds. The Veterinary Journal, 198, 203–210.

Tonnessen R., Borge K.S., Nodtvedt A., Indrebo A. (2012): Canine perinatal mortality: A cohort study of 224 breeds. Theriogenology, 77, 1788–1801.

Urfer S.R. (2009): Inbreeding and fertility in Irish Wolfhounds in Sweden: 1976 to 2007. Acta Veterinaria Scandinavica, 51, 21–32.

Voges S., Distl O. (2009): Inbreeding trends and pedigree analysis of Bavarian mountain hounds, Hanoverian hounds and Tyrolean hounds. Journal of Animal Breeding and Genetics, 126, 357–365.

Wang S., Leroy G., Malm S., Lewis T., Strandberg E., Fikse W.F. (2016): Merging pedigree databases to describe and compare mating practices and gene flow between pedigree dogs in France, Sweden and UK. Journal of Animal Breeding and Genetics, 134, 152–161.

Windig J.J., Oldenbroek K. (2015): Genetic management of Dutch golden retriever dogs with a simulation tool. Journal of Animal Breeding and Genetics, 132, 428–440.

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