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Genetic variation in aggression-related traits in Golden Retriever dogs

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Abstract

In this study, heritabilities of several measures of aggression were estimated in a group of 325 Golden Retrievers, using the Restricted Maximum Likelihood method. The studied measures were obtained either through owner opinions or by using the Canine Behavioural Assessment and Research Questionnaire (CBARQ). The aim of the study was to determine which of the aggression measures showed sufficient genetic variation to be useful as phenotypes for future molecular genetic studies on aggression in this population. The most reliable heritability estimates seemed to be those for simple dog owner impressions of human- and dog-directed aggression, with heritability estimates of 0.77 (S.E. 0.09) and 0.81 (S.E. 0.09), respectively. In addition, several CBARQ-derived measures related to human-directed aggression showed clear genetic differences between the dogs. The correlation between the estimated breeding values for owner impressions on human- and dog-directed aggression was relatively low. The low correlation suggests that these two traits have a partially different genetic background. They will therefore have to be treated as separate traits in further genetic studies.

Keywords: Dogs; Aggressive behaviour; Questionnaire; Heritability; Estimated breeding values

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1. Introduction

According to the breed standard, Golden Retriever dogs should have an ideal character to make good family pets. For example, the Dutch Golden Retriever Club breed standard states that Golden Retrievers are "good-natured, friendly, and confident" (GRCN, 2005). However, there are also reports of very aggressive Golden Retrievers (Edwards, 1991; Galac and Knol, 1997; Heath, 1991; Knol and Schilder, 1999). A genetic background has been suggested for this aggression because the behaviour seems to occur more often in certain Golden Retriever family groups (Knol et al., 1997). Consequently, a study on the genetics of aggressive behaviour in Golden Retrievers was started at the Utrecht University in 1997. The aim of this project is to identify mutations or polymorphisms in genes underlying the individual variation in aggressive behaviour in Golden Retrievers.

The key to success in any genetic study is the availability of a reliable and valid method for phenotyping. Obtaining phenotypes is especially challenging for behavioural traits, because of their complexity with many contributing factors (e.g., Mackenzie et al., 1986). Two main methods exist for phenotyping canine aggression: behavioural tests and questionnaires. In behavioural tests dogs are evaluated for their responses towards various stimuli under controlled conditions by trained evaluators. When using questionnaires, dog owners are asked opinions on the behaviour of their dog in various everyday situations. Examples of the first method include the aggression test developed by Netto and Planta (1997), and of the latter method the Canine Behavioural Assessment and Research Questionnaire (CBARQ) developed by Hsu and Serpell (2003). Data obtained with either method have thus far not been studied genetically, even though the aggression test was specifically developed for excluding aggressive individuals from breeding, and the CBARQ has been suggested to be a useful research tool for exploring the causes of behavioural problems in dogs.

In theory, behavioural tests are more objective than owner-derived information. The opportunities resulting from a shortened version of the aggression test of Netto and Planta (1997) to phenotypically characterise aggression in Golden Retrievers were studied by van den Berg et al. (2003, in press). These studies concluded that certain types of aggression cannot be elicited in the test and that the behaviour in a test may not be representative of the behaviour of the dog in everyday life. It is thus questionable if the aggression test could be used to reliably classify dogs into aggression classes in this population for genetic analyses. In contrast, the behavioural scores derived from the CBARQ seem to provide a promising tool for genetic studies of aggression in the Golden Retriever population (van den Berg et al., in press). However, before progressing to more complex and costly molecular genetic analyses it is important to determine the degree of heritability, i.e., the strength of the relationship between the genetic and phenotypic values, for the CBARQ scores in this population.

The aim of this paper was to estimate heritabilities of aggression-related measures obtained via the CBARQ on a population of Golden Retrievers in The Netherlands. More precisely, the goal was to study which measures of aggression that are available from the CBARQ show sufficient genetic variation to be interesting candidates for further molecular genetic studies on canine aggression in this population. Pearson product moment correlation coefficients were also calculated between the estimated breeding values for the most reliable human- and dog-directed aggression measures to provide an impression of the extent to which these two traits are genetically related to each other.

2. Materials and methods

2.1. Subjects

The data analyzed in this study were collected between 1997 and 2005 with the main target being family-based molecular genetic studies on aggression in the Dutch Golden Retriever population. It concerns 325 Golden Retrievers of which varying types of behavioural information was obtained. The dogs were recruited to the project either because of their aggressive behaviour (probands, $n = 159$) or because they were related to an aggressive dog (siblings and parents, $n = 166$). The group of recruited siblings and parents also included dogs that were aggressive according to their owners, as well as dogs that were non-aggressive according to their owners. Of the 325 dogs that had phenotypes available, 241 had a known pedigree containing at least three generations, through which 865 additional ancestral dogs without own phenotypes could be traced.

The phenotypic data included offspring of 108 known sires, with on average 2.3 offspring per sire (Fig. 1). The largest sire progeny group consisted of 14 offspring (including both full- and half-sibs), but the majority of sires only had one phenotyped offspring. These sires had been mated with 125 known dams, which had on average 1.9 offspring in the data (Fig. 2). Most dams also only had one phenotyped offspring, but the largest dam progeny group consisted of 10 offspring including both full- and half-sibs. Most of the

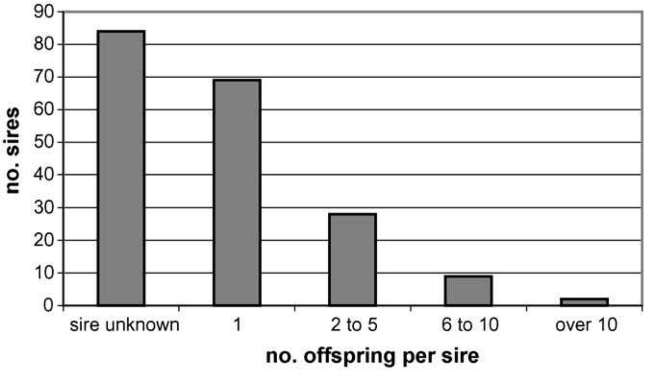

Fig. 1. Distribution of phenotyped offspring over sires.

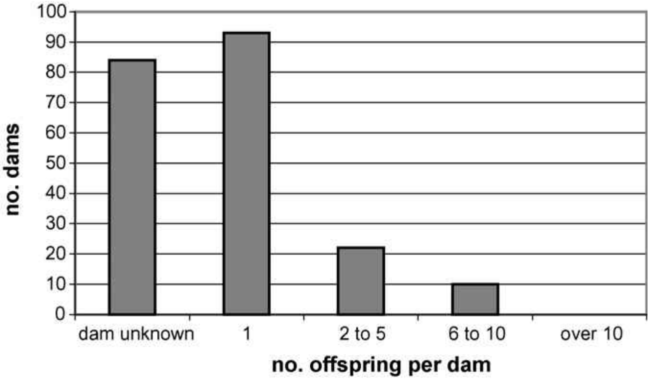

Fig. 2. Distribution of phenotyped offspring over dams.

other dam progeny groups consisted of only full-sibs. For 84 phenotyped dogs pedigree data was not available. The majority of the other dogs however were connected with other families in the data through their pedigrees.

2.2. Behavioural measures

Four types of behavioural measures were analyzed in this study. The first type was the owner impression. When a dog was recruited in the study, its owner was asked for his or her opinion on the aggressiveness of the dog (called later ‘‘owner impression’’; this is part of the ‘‘personal interview’’ that is mentioned in van den Berg et al., in press). Owners were asked if their dog was aggressive towards humans and if it was aggressive towards other dogs. The status of the dog was coded in three classes: non-aggressive (score 1), threatens (score 2), or bites (score 3). Almost all phenotyped dogs had the owner impression available on both human- and dog-directed aggression (Table 1).

Items of the CBARQ were the second type of behavioural measure that we analyzed. Most of the dog owners were asked to fill out the CBARQ. In contrast to the owner impressions, many owners completed the CBARQ several years after their first participation in the study (van den Berg et al., in press). The questionnaire included 27 items on the aggressiveness of the dog in various everyday situations (for more info on the CBARQ, see Hsu and Serpell, 2003). CBARQ items were scored with 5-point qualitative rating scales (i.e., 0 = no signs of aggression; 1–3 = moderate aggression, i.e., growling and baring teeth; 4 = serious aggression, i.e., snapping and biting). The majority of the dogs had CBARQ data available on all aggression-related items. The exception was aggression related to the behaviour of the dog towards other dogs in the same family, because only owners with multi-dog households could answer these items (Table 1).

So-called ‘‘shortened CBARQ scores’’ were the third type of behavioural measure that we analyzed. Hsu and Serpell (2003) demonstrated by means of factor analysis that the CBARQ aggression items can be grouped into stranger-directed aggression, owner-directed aggression, and strange dog-directed aggression. Consequently, the owners were asked to give answers to so-called ‘‘shortened CBARQ questions’’, where each question addressed one Hsu and Serpell factor directly (for more information on the shortened CBARQ questions and the reason why they were designed, see van den Berg et al., in press). The shortened CBARQ questions that we used here addressed the behaviour of the dog in the months prior to its first participation in the project. The shortened questions were therefore similar to the owner impressions, except that they separated human-directed aggression in aggression towards strangers and owners and that they were evaluated on a 5-point scale similar to the original CBARQ items. Shortened CBARQ questions were further converted into ‘‘shortened CBARQ scores’’ predicted by linear regression formulas that were described by van den Berg et al. (in press). These formulas were obtained by means of linear regression of CBARQ scores (calculated for the three aggression-related factors as the mean of the CBARQ items that were grouped in a factor by Hsu and Serpell; see van den Berg et al., in press) on shortened CBARQ questions. This was done to make the shortened CBARQ scores easier to compare with the original CBARQ scores. Answers to these questions were available for most dogs (Table 1).

Finally, we analyzed a fourth type of behavioural measure: CBARQ factors. In these factors, CBARQ scores and shortened CBARQ scores were combined so that original CBARQ scores were used when available, and regressed shortened CBARQ scores were used as an approximation of CBARQ scores for the deceased 83 dogs of which we had no CBARQ scores available. The CBARQ factors further include familiar dog-directed aggression in addition to the three types of aggression mentioned above. These factors were available for all dogs in the study except for familiar dog-directed aggression that was only available for dogs living in a household with more than one dog (Table 1).

2.3. Statistical analyses

Variance components needed for obtaining heritability estimates for the aggression measures were estimated with the Restricted Maximum Likelihood (REML) method (Patterson and Thompson, 1971),

Table 1
Abbreviations, descriptive statistics, and heritability estimates of 36 studied aggression measures

Aggression measure	Abbreviation	Descriptives						Heritability estimate	
		N	Mean[a]	S.D.	CV%	Min[a]	Max[a]	h^2	S.E.
Owner impressions									
Human-directed aggression	haggr	316	1.85	0.93	50	1	3	0.77	0.09
Dog-directed aggression	daggr	312	1.55	0.82	53	1	3	0.81	0.09
Original CBARQ items									
Verbal correction by owner	cb9	217	1.25	0.68	54	1	5	0.11	0.05
Strange adult approaching leashed dog	cb10	217	1.24	0.61	49	1	4	0.85	na[b]
Strange child approaching leashed dog	cb11	216	1.29	0.74	57	1	5	1.00	na[b]
Stranger approaching dog in car	cb12	206	1.38	0.92	67	1	5	0.07	0.09
Family member removing toy	cb13	217	1.48	1.02	69	1	5	0.32	0.17
Family member grooming dog	cb14	215	1.22	0.64	52	1	5	0.83	na[b]
Stranger approaching owner at home	cb15	217	1.25	0.60	48	1	4	0.13	0.06
Stranger approaching owner outside	cb16	217	1.18	0.50	42	1	4	0.57	0.09
Family member approaching eating dog	cb17	215	1.46	1.01	69	1	5	0.94	na[b]
Mailman visiting	cb18	215	1.52	0.82	54	1	5	0.03	0.06
Family member removing dog's food	cb19	207	1.40	1.05	75	1	5	0.95	na[b]
Stranger passing house with dog in yard	cb20	213	1.59	0.82	52	1	4	0.00	na[b]
Stranger trying to touch dog	cb21	217	1.30	0.72	55	1	5	0.99	na[b]
Cyclist passing house with dog in yard	cb22	213	1.40	0.73	52	1	4	0.00	na[b]
Unknown male dog appr. leashed dog	cb23	216	1.90	1.16	61	1	5	0.23	0.14
Unknown female dog appr. leashed dog	cb24	216	1.59	1.08	68	1	5	0.16	0.10
Family member staring at dog	cb25	216	1.07	0.35	33	1	4	1.00	na[b]
Unknown dog visiting dog's home	cb26	204	1.62	1.00	62	1	5	0.15	0.09
Cat entering garden	cb27	213	2.00	1.11	56	1	5	0.00	na[b]
Stranger visiting dog's home	cb28	217	1.21	0.51	42	1	4	0.44	0.05
Unknown dog barking/attacking dog	cb29	216	2.28	1.29	57	1	5	0.23	0.16
Family member stepping over dog	cb30	217	1.08	0.41	38	1	4	1.00	na[b]
Fam. member taking items stolen by dog	cb31	201	1.40	1.04	74	1	5	0.04	0.12
Aggression towards other family dogs	cb32	117	1.35	0.82	61	1	5	1.00	na[b]
Fam. dog appr. dog at favourite place	cb33	119	1.19	0.56	47	1	4	1.00	na[b]
Familiar dog appr. eating dog	cb34	119	1.92	1.26	66	1	5	0.71	0.39
Fam. dog appr. dog with favourite toy	cb35	118	1.85	1.11	60	1	5	0.26	0.24
Shortened CBARQ scores									
Aggression towards strange humans	scb5	241	0.47	0.47	100	0.13	1.66	0.90	na[b]
Aggression towards owners	scb6	241	0.50	0.53	106	0.12	1.57	0.88	na[b]
Aggression towards other dogs	scb7	241	1.09	0.93	85	0.29	3.19	0.31	0.10
CBARQ factors									
Stranger-directed aggression	stragg	264	0.42	0.56	132	0.01	3.41	0.87	na[b]
Owner-directed aggression	ownagg	264	0.40	0.61	153	0.01	2.89	0.82	na[b]
Dog-directed aggression	dogagg	264	0.94	0.98	105	0.01	4.01	0.43	na[b]
Familiar dog-directed aggression	fdgagg	115	0.65	0.86	133	0.01	4.01	0.45	na[b]

N, number of observations; S.D., standard deviation; CV%, coefficient of variation; Min, minimum value; Max, maximum value; h^2, heritability; S.E., standard error of heritability estimate.

[a] One was added to the original CBARQ items and shortened CBARQ scores for technical reasons. As a result of this, means and minimum and maximum values are higher than the values shown by van den Berg et al. (in press).

[b] Standard errors for estimates could not be obtained.

using univariate analyses and an animal model with the VCE4.2.4 software (Groeneveld, 1997). REML procedures are commonly used in quantitative genetics as they provide a powerful approach for analysing unbalanced data designs with complex known pedigrees (for more information on REML and variance component estimation, see, e.g. Lynch and Walsh, 1998). Best Linear Unbiased Prediction (BLUP) breeding values were further estimated for the dogs for owner impressions for human- and dog-directed aggression using PEST software (Groeneveld, 1994). Pearson product moment correlation coefficients were calculated between these two breeding values to get an indication of how these two traits are related to each other genetically, since estimating genetic correlations directly between the traits was not reasonable due to the small size of the data set.

The following linear animal model was assumed in the analyses for the owner impression traits:

$$y_{ijk} = \mu + \text{sex}_i + \text{age}_j + a_k + e_k$$

where y_{ijk} is the observed value for owner impression score for animal k, μ the general mean in the population, sex_i the fixed effect of the reproductive status i (i = 1–4, with 1 = intact male, 2 = castrated male, 3 = intact female, and 4 = castrated female), age_j the fixed effect of the age j (j = 1–11, with 1 = 0.5–1 year old, 2 = 1–2 years old, . . ., 10 = 9–10 years old, and 11 = over 10 years old), a_k the random additive genetic effect (i.e., breeding value) of the animal k, and e_k is the random residual effect related to the animal k. The age and reproductive status of the dogs had been recorded at the same time as the owner impressions.

For the other behavioural measures a similar linear animal model was used, but no fixed effects were included in the model. Some of the fixed effects considered in the mixed model included reproductive status and age, the origin of the dog (e.g., shelter, breeder, private), and various effects related to the relationship of the owner with the dog (e.g., participation in obedience courses; ways to react to misbehaviour of the dog). The majority of the fixed effects did not have any effect on the genetic parameter estimates of the aggression measures and were therefore excluded from the final model. This does not necessarily mean that these effects do not influence canine aggression, but is rather the result of a poor distribution of dogs over most fixed effect classes. In addition, inclusion of fixed effects into the model caused serious overfitting problems due to the small size of the data set (115–264 observations depending on the measure in question). Consequently, in this paper we present for the CBARQ traits only results estimated with a model that did not include any fixed effects in addition to the general mean.

In all analyses, distributions of animal effects and residuals were assumed to be multivariate normal with zero means and with $\text{Var}(a) = A\sigma_a^2$ and $\text{Var}(e) = I\sigma_e^2$, where A is the numerator relationship matrix and I is an identity matrix. All random effects were assumed to be mutually independent.

3. Results

The means, standard deviations, coefficients of variation and minimum and maximum values of all studied aggression measures are presented in Table 1. The distributions of observations were skewed for most of the aggression measures so that the majority of dogs classified in the lower (less aggressive) classes and only a few dogs had been classified in the most extreme (aggressive) classes. This was especially true for the original CBARQ items. Consequently, the means of the aggression measures were low and standard deviations fairly high, resulting in very high coefficients of variation for most measures. The owner impressions had the best distributions with a substantial number of dogs classified also in the more aggressive classes. The distributions of the shortened CBARQ scores and the CBARQ factors were quite flat, which was probably due to the way these measures were formed by regressing from the original CBARQ items.

The effect of reproductive status on owner impressions for human-directed aggression was moderate, with a difference of 0.72 scores between the two extreme reproductive status classes (Fig. 3). Castrated males had the highest scores for human-directed aggression, i.e., they were evaluated as the most aggressive. Reproductive status had a much smaller effect on dog-directed

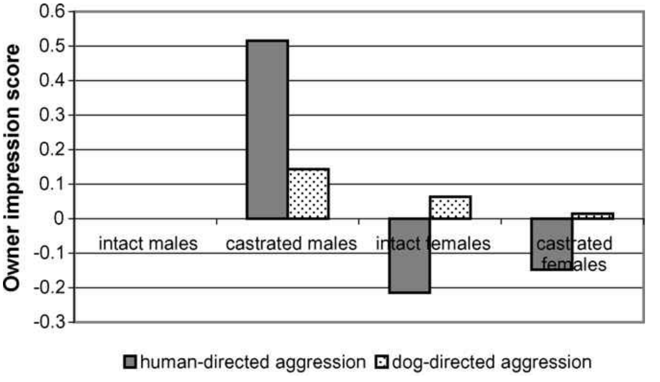

Fig. 3. Effect of reproductive status on owner impressions on human- and dog-directed aggression, expressed relative to scores for intact males.

aggression, with a difference of 0.14 scores between the two extreme reproductive status classes. Again, castrated males had been evaluated as the most aggressive, while intact males were evaluated even slightly less aggressive than castrated and intact females.

The effect of age on owner impressions for human-directed aggression was considerably higher than the effect of reproductive status (Fig. 4). The difference between the two extreme age classes was 1.32 scores. The owners had evaluated the youngest dogs as the most aggressive towards humans. From age class 5 onwards there was almost no difference between the age classes for owner impression on human-directed aggression. For dog-directed aggression there were no clear differences between the age classes, and the effect of age was also smaller in whole with a difference of 0.59 points between the two extreme age classes.

The heritability estimates for the aggression measures varied for the full possible range between 0 and 1 (Table 1). There were in total five measures (all CBARQ items) that had heritability estimates of 1.00. In addition, 11 measures (two owner impressions, five CBARQ items, two shortened CBARQ scores and two CBARQ factors) had heritability estimates over 0.75. Unfortunately, standard errors could not be obtained for the high heritability estimates of CBARQ items, shortened CBARQ scores and CBARQ factors. Consequently their reliability is

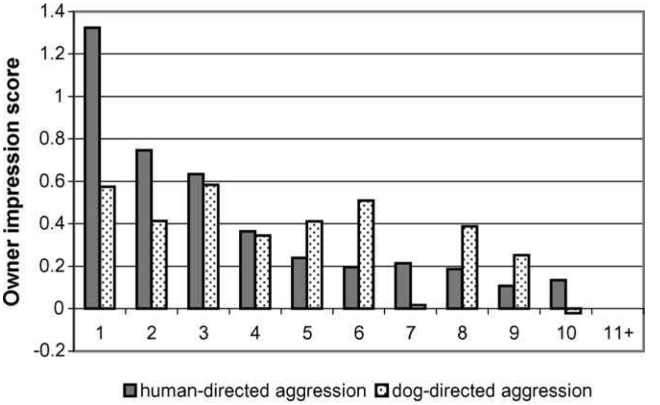

Fig. 4. Effect of age on owner impressions on human- and dog-directed aggression, expressed relative to scores for dogs over 10 years of age.

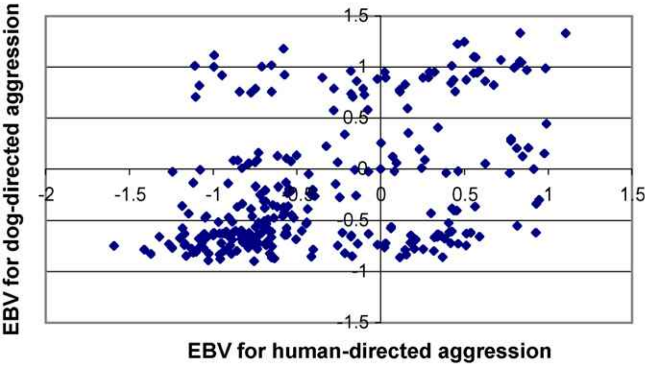

Fig. 5. Relationship between the estimated breeding values (EBV) for owner impressions on human-directed aggression and dog-directed aggression.

somewhat questionable, or at least it cannot be assessed properly. The most reliable heritability estimates were obtained for the owner impressions on human- and dog-directed aggression. Both estimates were very high, 0.77 and 0.81, respectively, and they had fairly low standard errors (0.09).

The Pearson product moment correlation coefficient between the BLUP breeding values for owner impressions on human- and dog-directed aggression was 0.40. Although the Pearson correlation somewhat underestimates the true genetic correlation due to inaccuracies in estimating the breeding values, this rather low value suggests that human- and dog-directed aggressions are genetically different although partially related traits. This relationship between the traits is also demonstrated in Fig. 5, where the estimated breeding values for human- and dog-directed aggression are plotted against each other.

4. Discussion

The high aggression scores of castrated males relative to intact males most likely result in this study from the common practice of castrating aggressive dogs in the hope that they will become less aggressive. The results suggest that aggressive behaviour influences castration decisions more in males than females, as there was little difference in aggression scores between castrated and intact females. We estimated the effect of reproductive status with a mixed model, so it is corrected for the effects of the age of the dog and the genetic effects. The estimated castration effect suggests that, even after castration, the owners judged male dogs that were castrated due to aggression as more aggressive than dogs that had not been considered aggressive enough to warrant castration in the first place. Neilson et al. (1997) also reported that castration is only effective in decreasing aggressive behaviour in less than a third of dogs. Similar observations on the relationship between the reproductive status and aggressive behaviour have been made, e.g. by Podberscek and Serpell (1996) in English Cocker Spaniels and Reisner et al. (2005) in English Springer Spaniels. In the study of Podberscek and Serpell, the significant positive association between neutering and aggression largely disappeared when dogs neutered specifically because they had been aggressive were removed from the analysis. Reisner et al. observed that castration was often the result of aggressive behaviour rather than a contributing cause, especially in male dogs.

The effect of age on the aggression scores in this study, with dogs under 2 years being the most aggressive, is partially related to the recruiting method of dogs rather than a pure age-effect. Owners usually encountered aggression problems and entered the study when their dog was approaching social maturity at 1.5 years of age, while the non-aggressive relatives were often recruited when they were older. However, similar onset of problem behaviour was also observed by Lund et al. (1995) in their study on behavioural problems including several forms of aggression in different dog breeds in Denmark. In addition, Guy et al. (2001) reported the highest frequency of biting behaviour towards owners in dogs less than 1 year of age in their study on Canadian dog populations. On the other hand, in the study of Reisner et al. (2005) dogs older than 3 years were significantly more aggressive towards their owners than younger dogs, but they specifically attempted to study aggressive behaviour past the age of social maturity.

At first glance the very high heritabilities obtained in this study for many of the aggression measures seem to point to a fairly simple genetic background for at least human-directed aggression in the studied population of Golden Retrievers. However, the results should be approached with some caution because the size of the data set is very small for variance component estimation, even with the inclusion of the pedigree structure. The poor data structure with unbalanced distributions of most measures further adds to the problem, since the REML method assumes normally distributed traits, although it is also quite robust against distribution violations. At most, we feel that the heritability estimates suggest that for instance cb10 (CBARQ item about aggression when a strange adult approaches the leashed dog) reveals more genetic differences in aggression between the dogs than cb9 (CBARQ item about aggression when verbally corrected by the owner). Their absolute values should not be taken as being the true value.

Based on the heritability estimates, the best behavioural measures for further genetic studies seem to be the owner impressions on human- and dog-directed aggression. The distributions of the owner impression traits were the best suited for variance component estimation using the REML method. The number of observations was also the highest for these two measures, and they could be fitted with proper mixed animal models. Consequently, these heritability estimates are more reliable than the estimates for any of the CBARQ-derived measures. A practical advantage of using these measures for phenotyping is that it is relatively easy and cheap to obtain owner impressions.

The good performance of the owner impressions relative to the more objective CBARQ based measures is somewhat surprising. Usually owners are not considered skilled enough in observing behaviour of their dogs, so that using their impressions might lead to biased results (Galac and Knol, 1997; Hart, 1995; van der Borg et al., 1991). In addition, information provided by owners is likely to reveal only a limited number of phenotypic classes (such as ‘‘aggressive’’ and ‘‘non-aggressive’’), while a more detailed classification might be needed for genetic studies (van den Berg et al., 2003). However, for this data set, classifying the dogs in only three classes seemed to be sufficient. The ‘‘generalness’’ of the owner impressions might have actually gotten more information out of the very small data set rather than the more detailed classification of the CBARQ related measures. Aggressive behaviour is also very salient for owners, so it might be relatively easy to evaluate.

Other potential candidate measures for further studies could also be some of the original CBARQ items with very high heritability estimates (e.g., cb10, cb11, cb16 and cb21 that are related to stranger-directed aggression, and cb14, cb17, cb19, cb25 and cb30 that are related to owner-directed aggression; Table 1). The shortened CBARQ scores about stranger- and owner-directed aggression and the CBARQ factors for stranger- and owner-directed aggression can also be considered because they had similarly high heritability estimates. In fact, the measures cb10, cb11, cb16 and cb21 are included in the factor for stranger-directed aggression, and the measures cb14, cb17, cb19, cb25 and cb30 are included in the factor for owner-directed aggression (van den Berg et al., in press), which may explain their similar heritability estimates. Although the standard errors of these very high heritability estimates could not be obtained, they seem to point to clear genetic differences between the dogs with respect to human-directed aggression. For studying dog-directed aggression the CBARQ-derived measures are not good enough, as none of them (CBARQ items, shortened scores or factors) seems to be able to pick up the genetic differences between the dogs as well as the owner impression.

Using the original CBARQ items for genetic studies is not totally straightforward, as they describe only one specialized possible expression of aggressive behaviour at a time. Consequently, if CBARQ items were to be used for further genetic studies on human-directed aggression in this data set, it might be more recommendable to use the shortened CBARQ scores or the CBARQ factors for stranger- and owner-directed aggression. However, using these combined measures for genetic studies can be problematic as well: they might mask the ‘‘true’’ genetic background of the studied traits because they combine information from many different sources that can be partially contradictory. If a larger data set could be obtained, it would be very interesting to investigate whether the genetic and phenotypic correlations between the original CBARQ items match the structure of the factors. Despite the problems, in the long term the CBARQ-derived measures seem very interesting for genetic studies of dog behaviour.

Conclusions that can be drawn from the present study are limited for two reasons. First, and perhaps most importantly, a larger data set is necessary for reliable quantitative genetic analyses. Such data set should include at least 500–1000 dogs with known phenotypes. From a data set of this size it becomes possible to study the genetic effects of behavioural traits that have a much smaller genetic component than Golden Retriever aggression. Examples from literature include hunting behaviour in Finnish Spitz (Karjalainen et al., 1996), Finnish Hound (Liinamo et al., 1997), German Short- and Wire-haired Pointers and Breton (Brenøe et al., 2002) and Flat-coated Retriever (Lindberg et al., 2004), and other working behaviour traits in German Shepherd and Labrador Retriever (Wilsson and Sundgren, 1997; Ruefenacht et al., 2002; Strandberg et al., 2005).

Second, for quantitative genetic studies one should probably avoid selective sampling of dogs as occurred in this study. We only collected information from aggressive dogs and their close relatives, but we did not sample all descendants of the sires and dams. This would require cooperation of more breeders and owners, which is often difficult to achieve. For family-based molecular genetic studies, it is not necessary to sample such a large number of progeny. However, the selective sampling might bias the results of quantitative genetic studies. Before any generalisations can be made, the results need to be confirmed with more research on a larger data set and in different breeds.

5. Conclusion

The owner impressions on human- and dog-directed aggression seem to be the best candidate measures for further genetic studies. They had very high heritability estimates, low standard errors, and the best data quality. Human- and dog-directed aggression seem to be genetically different although partially related traits. They should therefore be considered separately in further molecular genetic studies.

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