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The interaction between behavioural traits and demographic and management factors in German Shepherd dogs

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Abstract

As companion animals, a dog's lifestyle is mainly determined by its owner. Discrepancies between the dog's preferences and the owner's lifestyle might lead to the occurrence of unwanted behaviours that affect both the owner-dog relationship and the dog's welfare. The aim of this study was to identify behavioural traits that are characteristic of German Shepherd dogs (GSDs), and to analyse the relation between behavioural traits and demographic and management factors. Dog owners from the UK and Sweden were asked to complete two surveys, the established C-BARQ behavioural survey and a lifestyle survey developed for the study. A principal component analysis was applied to determine behavioural components for GSDs. Fifteen components were found to sufficiently explain the variance in the responses to C-BARQ, with the components Stranger-directed aggression and Dog-directed aggression explaining the greatest proportion of the variance in the data (12% and 10%, respectively). Linear models were then applied to assess the relationship between behaviour components and lifestyle factors using backward elimination to identify the model that best predicted the behaviour component. The cohort (UK or Sweden) and the age of the dog were associated with the highest number of behaviour components. This study showed that various demographic and management factors were associated with the expression of behavioural traits in GSDs. Results from this analyses may help to understand the interaction between the expression of external factors and dog behavioural traits and thus, improve the well-being of dogs and owners by reducing problem behaviours.

Keywords: C-BARQ; behaviour components; lifestyle; working dog

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1 Introduction

Extensive morphological and behavioural variability exists in purebred dogs, making certain breeds more suitable for specific tasks such as herding, guarding or hunting, while others are more suited as pets (Galibert et al., 2011; Mehrkam and Wynne, 2014). However, breed popularity analyses show that the dog's appearance is a more important factor for breed acquisition in pet dogs than functionality, behavioural traits or compatibility with the owner's lifestyle (Ghirlanda et al., 2013). A genetic predisposition to express particular patterns of behaviour together with unfavourable lifestyle factors may cause unwanted behaviours (e.g. aggression towards people, separation anxiety) that can have negative consequences for both owner (Casey et al., 2014) and dog (Rooney and Bradshaw, 2014; Roth et al., 2016) and in some cases lead to relinquishment of affected dogs to animal shelters or other homes (Cannas et al., 2017; Salman et al., 2000).

To address this issue, various studies have attempted to identify risk factors for unwanted behaviours by analysing the association between demographic factors (sex, neuter status, shape, litter size and weaning age) and management factors (training methods, housing and human contact) with dog behaviour (Blackwell et al., 2008; Casey et al., 2014; Deldalle and Gaunet, 2014; Haverbeke et al., 2008; McGreevy et al., 2013; Rooney and Cowan, 2011; Serpell and Duffy, 2016; Tiira and Lohi, 2015). Most of these studies concentrated either on single factors or multiple factors, but just one specific component of behaviour (e.g. aggression, fear). Lofgren et al. (2014) conducted a more comprehensive study on the interaction between multiple behavioural traits and a range of demographic and management factors in Labrador Retrievers. Results from that study highlighted the strong association between behaviour and management factors and suggested the value of investigating these factors in more detail and in additional breeds.

The German Shepherd dog (GSD) is one of the most popular dog breeds worldwide and is used as both pet and working dog. However, a drop in the UK GSD population has been observed in the last years and aggressive behaviour has been identified as one of the possible causes for the breed's diminishing popularity (O'Neill et al., 2017). Furthermore, the observation was made that about 30% of GSDs bred for the Swedish armed forces that were raised in foster families had to be re-homed to

another foster home at least once during their first 18 months of life (Wilsson, 2016). High scores for 'Confidence' and 'Engagement' temperament traits were identified as major risk factors for re-homing. A better understanding of the relationship between demographic and management factors and the expression of behavioural traits may help to reduce behaviour problems in this breed and in pet dogs more generally.

The present study describes behavioural traits in GSDs using the Canine Behaviour and Research Questionnaire (C-BARQ) (Hsu and Serpell, 2003), which has been shown to successfully characterize dog behaviour across breeds and countries (reviewed in Wiener and Haskell, 2016). We then further developed the approach of Lofgren et al. (2014) by developing a survey that assessed demographic and management factors in more detail and used it to investigate the relation between these factors and behavioural traits in GSDs.

2 Material and methods

2.1 Dogs

This study was conducted on GSDs from the UK and Sweden. To acquire participants for the UK cohort, the link to the online questionnaires was sent via email by the UK Kennel Club (KC) to all GSDs registered with the KC that were at least two years old. Additionally, GSD owners were also approached at dog shows and via breed clubs. Participating GSDs from the UK cohort were primarily pet dogs. All GSDs from the Swedish cohort were bred within the breeding program of the Swedish Armed Forces (SAF) with the purpose of becoming working dogs. Briefly, puppies were raised at the SAF, weaned at the age of 8 weeks and then fostered by members of the Swedish public (Wilsson and Sinn, 2012). After a behaviour test at the age of 15-18 months, dogs started working with the SAF, Swedish Police or other authorities or companies, and/or were selected as breeding animals, whereas others were kept as companion animals. For the Swedish cohort, owners, trainers or handlers of GSDs bred within the breeding program of the SAF were invited via email or letter to participate in the study.

2.2 Surveys

The C-BARQ consists of 101 questions related to (1) training and obedience, (2) aggression, (3) fear and anxiety, (4) separation-related behaviour, (5) excitability, (6) attachment and attention seeking, and (7) miscellaneous behaviours, e.g., chasing, urination (Duffy and Serpell, 2012). The initial C-BARQ was extended by 15 further questions to assess the dog's playfulness (Svartberg, 2005) and 21 of the miscellaneous C-BARQ questions were removed (Arvelius et al., 2014), leading finally to 95 questions. Responses were recorded on a 0-4 scale, with higher scores indicating increasing intensity of the expressed behaviour. A Swedish version of C-BARQ that had been translated and tested on Swedish dog owners previously (Svartberg, 2005) was used for the Swedish cohort.

Based on the results of our previous study (Lofgren et al., 2014), a second survey was developed (termed the 'lifestyle survey') to assess demographic and management factors of the dogs. The lifestyle survey comprised questions concerning demographic factors of the dog (e.g., sex, neuter status, age), its living situation (number of children, adults and other animals living with the dog, where the dog is housed) and its management (puppy socialisation, exercises and stimulation, training, activities). Preliminary testing was conducted for the lifestyle survey to ensure comprehensibility and clarity of the questions. The lifestyle survey was also translated into Swedish for use in the Swedish cohort. The English version of the lifestyle survey for the UK dogs is provided in the supplemental material (Supplement 1).

2.3 Quality control of survey data

The C-BARQ and the lifestyle survey were completed for 1,041 dogs (UK = 426, Sweden = 615) that met two criteria: registered with the KC (either UK or Swedish) and at least 2 years old. C-BARQ allows the option "not observed/not applicable" for behaviours that could not be observed. Those answers were handled as missing values. There were 299 dogs that had no missing values across all items, whereas 742 had one or more missing values.

The response rate for each C-BARQ question was calculated. Based on Hsu and Serpell (2003), questions with a response rate < 85% were excluded, which was the case for four questions related to

aggressive behaviour between dogs in the same household and thus were not applicable for owners with only one dog.

Lifestyle survey responses were also checked for completeness. Factors with excessive missing responses were excluded from subsequent analyses. Factors excluded were the dog's role as "companion" (no translation into Swedish available), age of neutering, coat length, whether the dog would be used for breeding, litter size (reliable data available for the Swedish cohort only), the working dog status (missing for 115 Swedish dogs), the type of working dog (not available for non-working dogs) and the puppy socialisation status (unknown for 235 dogs). In a subsequent analysis, several factors of particular interest that were excluded from the full data set due to a high number of missing responses (litter size, working dog status and the level of socialisation as a puppy) were considered in the statistical model using reduced data sets (only including dogs with complete responses for the relevant factor).

2.4 Characterisation of GSD behavioural traits

Responses from the C-BARQ survey were used to define the dog's behaviour in two ways: (I) by calculating behavioural components specifically for the GSD (GSD_{Comp}) and (II) by calculating scores for general behaviour components (Dog_{Comp}). The latter is a set of components that has been defined for and used in studies of multiple dog breeds by Duffy and Serpell (2012) and also includes the three play-related traits Dog directed interest, Human-directed play interest and Stranger-directed interest defined by Svartberg (2005). While GSD_{Comp} were used in the subsequent analyses of the interaction between behavioural traits and demographic and management factors, we also calculated the Dog_{Comp} to enable behavioural traits comparisons with other studies.

To calculate the GSD_{Comp}, a principal component analysis (PCA) was applied to the data to condense the 95 questions to a smaller number of components. GSD-specific components (principal components) were calculated for two main reasons: the original C-BARQ survey was extended with the inclusion of 15 playfulness-related questions and the average scores for the Dog_{Comp} showed non-normal distributions that could lead to difficulties in subsequent analyses. Prior to running the PCA,

several procedures (Cattell's scree-test, Horn's Parallel test and the Very Simple Structure (VSS) criterion) were applied and implemented using the R package 'psych' to identify the optimal number of components that capture the important information (Abdi and Williams, 2010), which gave a value of 15 for all tests. The PCA was then run for 15 principal components, followed by a varimax (orthogonal) rotation (for more information see Abdi and Williams, 2010). Missing values in the data set were replaced by the median value. Referring to Comrey and Lee (1992), questions that had loadings > |0.55| were considered as 'relevant' for the particular component and were used for labelling the components. Furthermore, this threshold was used for a subsequent filtering step: for each component the percentage of missing values of relevant items was calculated per dog. As suggested by Duffy and Serpell (2012), dogs with missing values for >20% of the relevant questions per component were excluded from this component. The dog's scores for the 15 components were considered as behaviour phenotypes in the following analysis (GSD_{Comp}).

To calculate the Dog_{Comp}, the average score on a scale from 0 to 4 was calculated across questions for 16 previously-defined traits (trainability, stranger-directed aggression, owner-directed aggression, stranger-directed fear, non-social fear, dog-directed aggression, dog-directed fear, touch sensitivity, separation-related behaviour, excitability, attachment/attention seeking, chasing, energy level, dog directed interest, human-directed play interest and stranger-directed interest). The component dog-rivalry was excluded due to an excess of missing records (refers to multiple dogs living in the same household). As described above, if >20% of the records for questions in a component were missing, this component was not calculated for the particular dog (Duffy and Serpell, 2012).

2.5 Characterisation of demographic and management factors

Some demographic and management factors were transformed and summarized prior to statistical analysis to simplify the analyses and to reduce the number of correlated factors considered in the models. Numbers of animals and dogs in the household were transformed into binary factors (presence of other dogs and animals = 1, absence =0). The commands a dog was trained for were summarized into a numerical factor "Number of commands". The interaction between sex and neuter

179 status has been found to be associated with behaviour in dogs (Casey et al., 2014) and thus, this factor
180 was also considered in the statistical analysis.

181 To avoid overfitting of the factors in the statistical analysis, the options for the four multiple choice
182 questions in the lifestyle survey were condensed using PCA. These included the following four
183 questions: "Role" (How do you see your dog?); "Comp" (Which of the following competitions has
184 your dog participated in?); "Train" (Which of the following training methods do you use?); and "Soc"
185 (Which of the following events was your dog socialised with as a puppy?). The same PCA protocol
186 was used as for the C-BARQ items: (I) the appropriate number of components was determined, (II)
187 the PCA was run using varimax rotation and (III) factors with a loading $\geq |0.55|$ were considered as
188 relevant and used for labelling the component. The PCA suggested a number of key components
189 describing the level of puppy socialisation, the role of the dog, the competition profile and training
190 method. Further details are given in the results section below.

191 In total, 28 demographic and management factors were taken into account to analyse the full data set
192 plus three factors considered in the reduced data sets ("Working dog", "Litter size" and "Soc_PC1"),
193 respectively. An overview of all demographic and management factors is given in Supplement 2. To
194 explore the interaction between numeric, ordinal and binary demographic and management factors,
195 Pearson (numeric-numeric), polyserial (numeric-ordinal) and polychoric (ordinal-ordinal) correlations
196 were calculated for the particular factor types as implemented in the 'hetcor' function in R.

197 ## 2.6 Influence of demographic and management factors on GSD behavioural traits

198 The effect of demographic and management factors on GSD_{Comp} was analysed using linear models.
199 To identify factors associated with the behaviours, all demographic and management factors were
200 initially fitted as fixed effects (initial model) in R. Then backward elimination implemented in the
201 'stepAIC' function of the R package 'MASS' was applied by removing one factor at a time to select
202 the model with the lowest Akaike information criterion (AIC) (final model). The variance explained
203 by the final model was calculated using the function 'Dsquared' in the R package 'modEvA' (Barbosa
204 et al. 2013). Across the 15 GSD_{Comp}, the average number of dogs included per model for the full data

set was 933 (range = 850-968). Sizes of the reduced data sets were: 835 (range = 756 – 868) for "Working dog status", 548 (range = 517 – 559) for "Litter size" and 728 (range = 660 – 758) for "Socialisation status".

3 Results

3.1 Characterisation of behavioural traits in GSDs

PCA was used to generate GSD-specific behavioural traits (GSD_{Comp}, Supplement 3). The 15 components (in descending order for the proportion of variance explained by the PCA) were labelled according to the relevant items as "Stranger-directed aggression" (positive loadings of aggressive behaviour towards strangers), "Dog-directed aggression" (positive loadings of aggressive behaviour and negative loadings of playfulness towards unfamiliar dogs), "Stranger-directed fear" (positive loadings of fearful behaviour towards strangers), "~~Playfulness~~Human-directed playfulness" (positive loadings of playful interaction with humans), "Resource guarding" (positive loadings of owner-directed aggression in regard to food or toys), "Excitability" (positive loadings of excited behaviour in response to different situations), "Separation anxiety" (positive loadings of stress-related behaviour when left alone), "Lack of obedience" (negative loadings of obedience-related behaviours), "Stranger-directed interest" (positive loadings of friendly interaction with strangers), "Attention seeking" (positive loadings of attention-seeking behaviour towards owner), "Chasing" (positive loadings of chasing-related behaviours), "Non-social fear" (positive loadings of fear response to loud noise or unfamiliar objects), "Dog-directed fear" (positive loadings of fearful behaviour towards unfamiliar dogs), "Aversion of being stepped over" (positive loadings of fearful or aggressive response when stepped over) and "Touch-sensitivity" (positive loadings of fearful behaviour when touched for various treatments). Descriptive statistics for GSD_{Comp} scores are shown in Table 1.

The Dog_{Comp} scores (ranging from 0 to 4) were calculated for each dog (Table 2). The highest average scores in GSDs were recorded for Human-directed play interest (3.15 ± 0.02; mean and standard error), followed by Trainability (2.63 ± 0.01) and Stranger-directed interest (2.34 ± 0.04). The lowest average scores were measured for Owner-directed aggression (0.08 ± 0.01), Stranger-directed fear

(0.15 ± 0.01) and Separation-related behaviours (0.20 ± 0.01). Touch-sensitivity had the greatest number of missing records and Dog rivalry was not calculated because of >20% missing values.

3.2 Description of demographic and management factors

There were a number of differences between the UK and Swedish GSDs regarding demographic and management factors (Supplement 2). The majority of UK GSDs lived together with other dogs or animals, whereas Swedish dogs were primarily kept without the presence of other animals. The majority of UK GSDs were neutered while the majority of Swedish GSDs were intact. Of the UK GSDs, 77.4% had been used for breeding (some of the GSDs were used for breeding before neutering, which accounts for the high levels of both neutered dogs and dogs used for breeding), whereas only 9.4% of the Swedish dogs had offspring. The Swedish dogs received more frequent training than the UK dogs, but participated less often in dog shows. Because of the differences between the populations, we considered analysing them separately. However, it was concluded that a single analysis would give greater statistical power, and that by fitting demographic and management factors and the cohort (for demographic and management factors that were not captured with the lifestyle survey) we sufficiently accounted for differences in the two cohorts.

The PCA of the multiple choice questions in the lifestyle survey resulted in one component for "Soc" (Soc_PC1), two components for "Role" (Role_PC1, Role_PC2) and "Comp" (Comp_PC1, Comp_PC2), and three components for "Train" (Train_PC1, Train_PC2, Train_PC3) (described in Supplement 3). Soc_PC1 is described by high loadings for all puppy socialisation options (highly positive scores equate to high socialisation status of the dog); Role_PC1 is described by high loadings for pet dog functions (highly positive scores equate to pet dog), Role_PC2 is described by high loadings for a specific function (highly positive scores equate to co-worker and highly negative scores to show dog); Comp_PC1 is described by high loadings for showing (highly positive scores equate to participation in dog shows and highly negative scores to no participation in competitions), Comp_PC2 is described by high loadings for participation in advanced obedience competitions (highly positive scores equate to advanced/ high level of obedience); Train_PC1 is described by high loadings for

positive reinforcement (highly positive scores equate to the use of positive reinforcement, highly negative scores equate to no training), Train_PC2 is described by high loadings for counterconditioning (highly positive scores equate to the use of counterconditioning) and Train_PC3 is described by high loadings for aversive training methods (highly positive scores equate to the use of aversive methods).

Results for the correlation analysis between the numeric and ordinal demographic and management factors are illustrated in Supplement 4. The correlations were low to moderate, with the highest correlations found for "People_hh" with "Children_hh" (0.63), "F_interaction_humans" with "F_interaction_dogs" (0.59), "Role_PC2" with "Comp_PC1" (-0.4), "Age.acquisition" with "Soc_PC1" (-0.35), "F_training" with "Commands" (0.36) and "Commands" with "Comp_PC2" (0.31).

3.3 Factors associated with behavioural traits in GSDs

Following backward elimination, the final models based on GLM explained on average 7.0% of the variance in the data. The maximum of 16.9% explained variance was found for Stranger-directed interest and the minimum of 1.3% explained variance for Excitability (Table 3). Out of the 15 GSD_{Comp}, the factors that appeared most frequently in the final models were "Cohort" and "Age" (9 GSD_{Comp}), "Commands", "Dogs_hh", "Gender*Neuter status" and "F_offlead" (7) (Table 3). As we used AIC for model selection, some factors with non-significant associations with GSD_{Comp} remained in the final models. However, the results presented primarily focus on demographic and management factors that were present as significant associations ($p < 0.05$) in the final models.

3.3.1 Environment

Figure 1 shows the adjusted effect size of "Cohort" from the fitted final models for the nine GSD_{Comp} where the factor "Cohort" appeared in the final model. For some of these traits, the effect directions were "favourable" (negatively associated with problem behaviours and positively associated with desired or neutral behaviours) in the UK cohort; these included lower scores for Dog-directed

aggression, Resource guarding, Lack of obedience, Dog-directed fear, Attention seeking and higher scores for Stranger-directed interest. For other traits the effect directions were favourable in the Swedish cohort, including lower scores for Stranger-directed aggression and Chasing and higher scores for ~~Playfulness~~Human-directed playfulness.

The presence of other dogs in the household ("Dogs_hh") had primarily a favourable association with GSD_{Comp}. With at least two dogs per household, scores for Dog-directed aggression, Resource guarding, Separation anxiety, Lack of obedience, Attention-seeking and Touch-sensitivity were lower compared to scores for dogs in a single-dog household (Table 3). The presence of other animals in the household ("Animals_hh") was also favourably associated with GSD_{Comp}, for example with lower scores for Stranger-directed fear and Chasing.

The living place of the dog was associated with Excitability and ~~Playfulness~~Human-directed playfulness. Dogs that live primarily outdoors had the highest scores for ~~Playfulness~~Human-directed playfulness but the lowest scores for Excitability (Figure 2).

3.3.2 Dog-related factors

Various demographic factors were associated with the GSD_{Comp}. While sex and neuter status did not appear as main effects in the final models, the interaction between sex and neuter status appeared among the factors in the final model for seven traits. Intact dogs had higher scores for Separation anxiety and lower scores for Non-social fear than neutered dogs for both males and females (Figure 3). In contrast, other GSD_{Comp} showed inconsistent results between the sexes. Neutered male GSDs had lower scores for Stranger-directed fear and ~~Playfulness~~Human-directed playfulness than intact male dogs, but the opposite pattern was seen for female dogs.

The dog's age was another factor occurring in the final model for several traits. With increasing age, scores for Stranger-directed aggression, Stranger-directed fear, ~~Playfulness~~Human-directed playfulness, Chasing, Non-social fear, and Dog-directed fear decreased while Dog-directed aggression increased. An association with coat colour was detected for Chasing with sable GSDs having higher

scores for Chasing than dogs with other coat colours (Figure 4). Litter size, which was analysed on a reduced data set, was not associated with any of the GSD_{Comp} in the final models.

3.3.3 Management and lifestyle

Participation in dog competitions ("Comp_PC1", "Comp_PC2") was favourably associated with some of the GSD_{Comp}. Dogs participating in dog shows (high scores for "Comp_PC1") had significantly lower scores for Stranger-directed aggression and Touch sensitivity. Dogs with high scores for the participation in advanced obedience competitions ("Comp_PC2") tended to have high scores for ~~Playfulness~~Human-directed playfulness. Likewise, the greater the number of commands a dog was trained for, the higher the scores were for ~~Playfulness~~Human-directed playfulness, Stranger-directed interest and the lower the scores were for Stranger-directed fear, Lack of obedience, Attention seeking and Non-social fear. High scores for the use of dog training including aversive and dominance based methods ("Train_PC3") was associated with low scores for Dog-directed aggression, Stranger-directed fear, and Aversion being stepped over.

Frequent interaction with humans or dogs was associated with decreased scores for aggression towards the respective species and also with increased scores for Stranger-directed interest in the case of frequent interaction with humans and with increased scores for Dog-directed fear in the case of frequent interactions with dogs. More frequent walks were associated with higher scores for Stranger-directed aggression and lower scores for Stranger-directed fear. The greater the amount of exercise the dog received per day, the higher were scores for Separation anxiety and Attention seeking. More frequent training and time off-lead during walks were associated with lower scores for Lack of obedience and Chasing.

The working dog status ("Working.dog") and the dog's socialisation as a puppy ("Soc_PC1") were analysed on reduced data sets due to a high number of missing values. The working dog status occurred twice in a final model of GSD_{Comp}: working dogs had higher scores for Excitability than non-working dogs (effect: 0.16, p-value = 0.06) and lower scores for Dog-directed aggression (effect: −0.16, p-value = 0.09). The factor "Soc_PC1" was accounted for in final model for seven traits. High

scores for socialisation as a puppy were significantly associated with lower scores for Excitability and higher scores for Stranger-directed interest and Chasing.

4 Discussion

In this study, we assessed demographic and management factors and analysed their contribution to the expression of behavioural traits in German Shepherd dogs (GSDs). We classified the responses given in a standard dog behavioural survey (C-BARQ) into behavioural traits that are characteristic for this dataset (GSD_{Comp}) and showed that various demographic and management factors are associated with these GSD_{Comp}.

4.1 GSD specific behavioural traits

The PCA suggests that 15 components (principal components) can be used to characterise the behaviour of GSDs. The resulting GSD_{Comp} (Supplement 2) are generally consistent with the behavioural traits described in Duffy and Serpell (2012) and Svartberg (2005) (Dog_{Comp}) across many breeds. Nevertheless, there are GSD_{Comp} that differed from the Dog_{Comp}: (1) C-BARQ items loading to the Dog_{Comp} Owner-directed aggression are divided into two GSD_{Comp}, Resource guarding and Aversion to being stepped over, and (2) the Dog_{Comp} Energy level was not identified as a GSD_{Comp} (the questions associated with Energy level had loadings < |0.55| for all of the GSD_{Comp}). The overlaps between GSD_{Comp} and Dog_{Comp} shown in this study support the consistency of Dog_{Comp} classified by Duffy and Serpell (2012), which has also been demonstrated in other studies (Berg et al., 2006; Duffy et al., 2008; Nagasawa et al., 2011).

However, the difference between the GSD_{Comp} and Dog_{Comp} lists indicate that breed-specific behavioural variation exists and that it can be identified with the C-BARQ survey. The same observation was made in Lofgren et al. (2014), where based on the C-BARQ survey, the novel traits Fetching and Barking tendency were identified as varying within Labrador Retrievers; these traits were not shown as behaviour components in other studies.

357 Dog_{Comp} for GSDs were in accordance with scores for GSDs reported in other studies. GSDs had high
358 average scores for Trainability, medium scores for Dog-directed aggression and Stranger-directed
359 aggression and low scores for Stranger-directed fear as in previous studies (Foyer et al., 2014;
360 Ghirlanda et al., 2013).

361 4.2 Factors associated with GSD behavioural traits

362 By applying linear models to fit the relationships between GSD_{Comp} and demographic and
363 management factors, we found that various factors were associated with the behavioural traits (Table
364 3), consistent with the widely recognized theory that the expression of behaviour is influenced by the
365 environment (reviewed in Sih et al., 2004). Because a dog shares the environment and lifestyle with
366 its owner, and these can differ substantially between individuals, there are many factors with a
367 potential influence on behavioural traits. This is indicated by our results, which showed that 27 out of
368 31 factors we examined were associated with at least one of the 15 GSD_{Comp}. However, we cannot
369 infer cause and effect for many of the associations and although many factors were taken into account
370 to analyse the described behavioural traits, they still only explained a small proportion of the variance
371 observed in the GSD_{Comp} (ranging from 1.3% to 16.9%), similar to the study of Casey et al. (2014).
372 There are presumably additional factors and experiences that contribute to behavioural differences
373 between dogs, e.g. whether the resting place was a dog basket, the sofa or the owner's bed (Cannas et
374 al., 2017), the style of playful interaction with the owner (McGreevy and Masters, 2008), and even the
375 owner's personality (Dodman et al., 2018), that were not assessed in this study.

376 The origin of the dog ("Cohort") was associated with eight out of the 15 GSD_{Comp}. Different
377 management regimes or demographic characteristics between GSDs from the UK and Sweden that
378 were not assessed in the lifestyle survey may be the cause of this effect or even 'cultural' differences
379 between British and Swedish dog owners that influenced how they responded to the survey. The
380 rearing of the dogs is likely to be a critical influence affecting behavioural traits. All Swedish GSDs
381 were reared under standardized conditions and had undergone frequent handling for behaviour and
382 health assessment as puppies (described in Foyer et al., 2013) while the rearing of UK GSDs

383 depended on the respective owner. Alternatively, the breeding (i.e. genetic) background of the dogs in
384 this study may play a large role. GSDs from the UK cohort are primarily pet dogs, whereas Swedish
385 dogs were all bred in a working dog program for the Swedish Armed Forces. Moreover, 77.4% of
386 GSDs from the UK were used for breeding compared to 9.4% of breeding dogs in the Swedish cohort,
387 which further indicates differences between the two cohorts.

388 To determine the effect of the dog's role as a working dog, this factor was analysed on a reduced data
389 set. While other studies detected multiple behaviour differences between working and non-working
390 dog breeds (Eken Asp et al., 2015; Lofgren et al., 2014; Mariti et al., 2013), the working dog status
391 was only associated with a single trait (Excitability) for the within-breed comparison conducted in this
392 study. However, because the Swedish cohort encompassed dogs selected as working dogs (although
393 not all were used as working dogs) while the UK dogs were mainly pets (only 5.6% working dogs),
394 the cohort factor might partly reflect this selection and thus also account for the working vs non-
395 working status of the dogs in this study. Further genetic investigation of the two cohorts may provide
396 insight into this issue.

397 No associations with GSD_{Comp} were found for "Sex" or "Neuter status" as separate factors in
398 accordance to other studies (Blackwell et al., 2008; Casey et al., 2014). Instead, the critical factor in
399 our study was the interaction between sex and neuter status, especially for fear-related GSD_{Comp}.
400 Although the causal relationship could not be revealed with data from this study, our results and
401 findings of other studies (Duffy, 2006; Farhoody, 2010; Kaufmann, 2017) indicate that neutering may
402 increase fear and insecurity. The increase in aggressive behaviour in neutered dogs described in
403 previous studies (Kaufmann, 2017; Podberscek and Serpell, 1996) could not be tested in this study,
404 however, fear and insecurity can be the underlying driving factors for aggressive behaviour (Eken Asp
405 et al., 2015).

406 The scores for aggressive or fearful behaviours were lower with increasing age, apart from aggressive
407 behaviour towards dogs, which increased. Other studies found an association between increasing age
408 and the reduction of problem behaviours, such as fear in response to sudden noises (Åkerberg et al.,
409 2012) as well as attention-seeking and separation-anxiety (Blackwell et al., 2008), but others observed

an increase of aggressiveness in older dogs (Bennett and Rohlf, 2007; Casey et al., 2014; Eken Asp et al., 2015). These inconsistent results indicates that over time, dogs will experience situations that alter the expression of certain behaviours. With increasing age, there is a higher likelihood of unfavourable individual experiences contributing to aggression or fear, but frequent training and positive interactions with humans or dogs might counteract this effect.

Training characteristics (level, frequency and method of training) were associated with several GSD_{Comp} in our study. We found that the different factors characterising the training level of a dog were positively correlated with each other (Supplement 4) and that a high training level (indicated by high scores for the participation in advanced obedience competitions "Comp_PC2", a high number of commands for which a dog was trained and frequent training) was primarily favourably associated with unwanted behaviours. This finding is consistent with a negative correlation between obedience training and the exhibition of problem behaviours and also with an improvement in obedience and performance with frequent training, as described in previous studies (Alexander et al., 2011; Bennett and Rohlf, 2007; Clark and Boyer, 1993; Jagoe and Serpell, 1996). Interestingly, high scores for the participation in advanced obedience competitions ("Comp_PC2") and a high number of commands for which a dog was trained, were also associated with high scores for ~~Playfulness~~Human-directed playfulness. The direction of causality between a high training level and the increased expression of playfulness remains unknown, but this association suggests several possibilities. Perhaps some aspect of the training experience promotes a positive emotional state in the dog, allowing playfulness to be expressed more often or maybe the playful interaction itself supports better learning abilities in dogs, as suggested by the study of Affenzeller et al. (2017). Another possibility is that owners choose to spend more time in training activities with more playful dogs.

~~Higher scores for aversive training methods ("Train_PC3") were associated with lower scores for unwanted behaviours (Dog-directed aggression, Stranger-directed fear and Dog-directed fear), but also with lower scores for Stranger-directed interest. Higher scores for positive reinforcement based training methods ("Train_PC1" and "Train_PC2") were associated with lower scores for Touch-sensitivity. The causal relationship between training methods and dog behaviour needs to be further~~

~~investigated, as it has been reported that the use of aversive methods can affect the dog's welfare by inducing stress (Deldalle and Gaunet, 2014) and suppress the dog's performance in obedience and "protection work" exercises (Haverbeke et al., 2008), while positive reinforcement methods have been suggested to positively influence the dog's learning ability (Rooney and Cowan, 2011).~~

Higher levels of daily exercise were associated with higher scores for Separation anxiety and Attention seeking. This is in agreement with a study by Mariti et al. (2013), which showed a trend across breeds for higher attachment of search and rescue dogs to their owners compared to non-working dogs. Parthasarathy and Crowell-Davis (2006) suggest that dogs that spend more time with their owners in intensive activities may be more prone to show separation-anxiety than dogs that spend less time in intensive activities with their owners, due to a specific attachment style of the former. However, other studies showed a favourable association between the levels of daily exercise and separation anxiety (Lofgren et al., 2014; Tiira and Lohi, 2015). The variance explained for GSD_{Comp} Separation anxiety by the associated demographic and management factors was <3%, indicating the complex nature of this trait and that there are other unmeasured factors that influence the expression of separation anxiety, e.g., time left alone (Rehn and Keeling, 2011).

5 Conclusions

Multiple factors are associated with behavioural traits in dogs, but the direction of the effect differs across studies (e.g. sex, neuter status) and these factors generally explain only a small amount of the variation in the behaviour. Considering the influence of the dog's age on many behavioural traits in this study, we conclude that individual experiences that were not captured by the lifestyle survey also play an important role. However, we observed that several management factors (e.g. the frequency of training, participation in dog competitions) had an overall favourable association that suggest these activities may reduce the risk of undesirable behaviours. The results presented here indicate that dog training rather than high levels of exercise *per se* may be key to modulating dog behaviour, indicating an influence of the owner-dog bond. The extent to which behavioural differences associated with cohort are due to environmental factors not accounted for in this study or genetic differences (e.g. due

to selection for working characteristics) needs further investigation. For future studies on behaviour characteristics in dogs, it will be useful to agree on key environmental and demographic factors to consider in analyses. This will help in identifying consistent findings across studies and ultimately may suggest improvements for dog management.

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References

Abdi, H., Williams, L.J., 2010. Principal component analysis. Wiley Interdiscip. Rev. Comput. Stat. 2, 433–459. https://doi.org/10.1002/wics.101

Affenzeller, N., Palme, R., Zulch, H., 2017. Playful activity post-learning improves training performance in Labrador Retriever dogs (Canis lupus familiaris). Physiol. Behav. 168, 62–73. https://doi.org/10.1016/j.physbeh.2016.10.014

Åkerberg, H., Wilsson, E., Sallander, M., Hedhammar, Å., Lagerstedt, A.-S., Larhammar, D., Meyerson, B., 2012. Test for personality characteristics in dogs used in research. J. Vet. Behav. Clin. Appl. Res. 7, 327–338. https://doi.org/10.1016/j.jveb.2012.01.007

Alexander, M.B., Friend, T., Haug, L., 2011. Obedience training effects on search dog performance. Appl. Anim. Behav. Sci. 132, 152–159. https://doi.org/10.1016/j.applanim.2011.04.008

Arvelius, P., Eken Asp, H., Fikse, W.F., Strandberg, E., Nilsson, K., 2014. Genetic analysis of a temperament test as a tool to select against everyday life fearfulness in Rough Collie. J. Anim. Sci. 92, 4843–4855. https://doi.org/10.2527/jas.2014-8169

Barbosa A.M., Real R., Munoz A.R., Brown J.A., 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers. Distributions 19, 1333-1338. https://doi.org/10.1111/ddi.12100

Bennett, P.C., Rohlf, V.I., 2007. Owner-companion dog interactions: Relationships between demographic variables, potentially problematic behaviours, training engagement and shared activities. Appl. Anim. Behav. Sci. 102, 65–84. https://doi.org/10.1016/j.applanim.2006.03.009

Berg, L. van den, Schilder, M.B.H., Vries, H. de, Leegwater, P. a. J., Oost, B.A. van, 2006. Phenotyping of Aggressive Behavior in Golden Retriever Dogs with a Questionnaire. Behav. Genet. 36, 882–902. https://doi.org/10.1007/s10519-006-9089-0

Blackwell, E.J., Twells, C., Seawright, A., Casey, R.A., 2008. The relationship between training methods and the occurrence of behavior problems, as reported by owners, in a population of domestic dogs. J. Vet. Behav. Clin. Appl. Res. 3, 207–217. https://doi.org/10.1016/j.jveb.2007.10.008

Cannas, S., Talamonti, Z., Mazzola, S., Minero, M., Picciolini, A., Palestrini, C., 2017. Factors associated with dog behavior problems referred to a behavior clinic. J. Vet. Behav. https://doi.org/10.1016/j.jveb.2017.12.004

Casey, R.A., Loftus, B., Bolster, C., Richards, G.J., Blackwell, E.J., 2014. Human directed aggression in domestic dogs (Canis familiaris): Occurrence in different contexts and risk factors. Appl. Anim. Behav. Sci. 152, 52–63. https://doi.org/10.1016/j.applanim.2013.12.003

Clark, G.I., Boyer, W.N., 1993. The effects of dog obedience training and behavioural counselling upon the human-canine relationship. Appl. Anim. Behav. Sci. 37, 147–159. https://doi.org/10.1016/0168-1591(93)90107-Z

515 Comrey, A., Lee, H., 1992. A First Course in Factor Analysis. Psychology Press, New York, USA.
516 Deldalle, S., Gaunet, F., 2014. Effects of 2 training methods on stress-related behaviors of the dog
517 (Canis familiaris) and on the dog–owner relationship. J. Vet. Behav. Clin. Appl. Res. 9, 58–
518 65. https://doi.org/10.1016/j.jveb.2013.11.004
519 Dodman, N.H., Brown, D.C., Serpell, J.A., 2018. Associations between owner personality and
520 psychological status and the prevalence of canine behavior problems. PLOS ONE 13,
521 e0192846. https://doi.org/10.1371/journal.pone.0192846
522 Duffy, D.L., 2006. Non-reproductive effects of spaying and neutering on behavior in dogs, in:
523 Proceedings of the Third International Symposium on Non-Surgical Contraceptive Methods
524 for Pet Population Control. Alexandria, Virginia.
525 Duffy, D.L., Hsu, Y., Serpell, J.A., 2008. Breed differences in canine aggression. Appl. Anim. Behav.
526 Sci. 114, 441–460. https://doi.org/10.1016/j.applanim.2008.04.006
527 Duffy, D.L., Serpell, J.A., 2012. Predictive validity of a method for evaluating temperament in young
528 guide and service dogs. Appl. Anim. Behav. Sci. 138, 99–109.
529 https://doi.org/10.1016/j.applanim.2012.02.011
530 Eken Asp, H., Fikse, W.F., Nilsson, K., Strandberg, E., 2015. Breed differences in everyday
531 behaviour of dogs. Appl. Anim. Behav. Sci. 169, 69–77.
532 https://doi.org/10.1016/j.applanim.2015.04.010
533 Farhoody, P., 2010. Behavioral and physical effects of spaying and neutering domestic dogs (Canis
534 familiaris). Master thesis. Hunter College.
535 Foyer, P., Bjällerhag, N., Wilsson, E., Jensen, P., 2014. Behaviour and experiences of dogs during the
536 first year of life predict the outcome in a later temperament test. Appl. Anim. Behav. Sci. 155,
537 93–100. https://doi.org/10.1016/j.applanim.2014.03.006
538 Foyer, P., Wilsson, E., Wright, D., Jensen, P., 2013. Early experiences modulate stress coping in a
539 population of German shepherd dogs. Appl. Anim. Behav. Sci. 146, 79–87.
540 https://doi.org/10.1016/j.applanim.2013.03.013

Galibert, F., Quignon, P., Hitte, C., André, C., 2011. Toward understanding dog evolutionary and domestication history. C. R. Biol., On the trail of domestications, migrations and invasions in agriculture 334, 190–196. https://doi.org/10.1016/j.crvi.2010.12.011

Ghirlanda, S., Acerbi, A., Herzog, H., Serpell, J.A., 2013. Fashion vs. Function in Cultural Evolution: The Case of Dog Breed Popularity. PLOS ONE 8, e74770. https://doi.org/10.1371/journal.pone.0074770

Haverbeke, A., Laporte, B., Depiereux, E., Giffroy, J.-M., Diederich, C., 2008. Training methods of military dog handlers and their effects on the team's performances. Appl. Anim. Behav. Sci. 113, 110–122. https://doi.org/10.1016/j.applanim.2007.11.010

Haverbeke, A., Messaoudi, F., Depiereux, E., Stevens, M., Giffroy, J.-M., Diederich, C., 2010. Efficiency of working dogs undergoing a new Human Familiarization and Training Program. J. Vet. Behav. Clin. Appl. Res. 5, 112–119. https://doi.org/10.1016/j.jveb.2009.08.008

Hsu, Y., Serpell, J.A., 2003. Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. J. Am. Vet. Med. Assoc. 223, 1293–1300. https://doi.org/10.2460/javma.2003.223.1293

Jagoe, A., Serpell, J., 1996. Owner characteristics and interactions and the prevalence of canine behaviour problems. Appl. Anim. Behav. Sci., Human-Animal Interactions 47, 31–42. https://doi.org/10.1016/0168-1591(95)01008-4

Kaufmann, C.A., 2017. The Social Behaviour of Neutered Male Dogs Compared to Intact Dogs (Canis lupus familiaris): Video Analyses, Questionnaires and Case Studies. Vet Med Open J 2, 22–37. https://doi.org/10.17140/VMOJ-2-113

Lofgren, S.E., Wiener, P., Blott, S.C., Sanchez-Molano, E., Woolliams, J.A., Clements, D.N., Haskell, M.J., 2014. Management and personality in Labrador Retriever dogs. Appl. Anim. Behav. Sci. 156, 44–53. https://doi.org/10.1016/j.applanim.2014.04.006

Mariti, C., Ricci, E., Carlone, B., Moore, J.L., Sighieri, C., Gazzano, A., 2013. Dog attachment to man: A comparison between pet and working dogs. J. Vet. Behav. Clin. Appl. Res. 8, 135–145. https://doi.org/10.1016/j.jveb.2012.05.006

McGreevy, P.D., Georgevsky, D., Carrasco, J., Valenzuela, M., Duffy, D.L., Serpell, J.A., 2013. Dog Behavior Co-Varies with Height, Bodyweight and Skull Shape. PLOS ONE 8, e80529. https://doi.org/10.1371/journal.pone.0080529

McGreevy, P.D., Masters, A.M., 2008. Risk factors for separation-related distress and feed-related aggression in dogs: Additional findings from a survey of Australian dog owners. Appl. Anim. Behav. Sci. 109, 320–328. https://doi.org/10.1016/j.applanim.2007.04.001

Mehrkam, L.R., Wynne, C.D.L., 2014. Behavioral differences among breeds of domestic dogs (Canis lupus familiaris): Current status of the science. Appl. Anim. Behav. Sci. 155, 12–27. https://doi.org/10.1016/j.applanim.2014.03.005

Nagasawa, M., Tsujimura, A., Tateishi, K., Mogi, K., Ohta, M., Serpell, J.A., Kikusui, T., 2011. Assessment of the factorial structures of the C-BARQ in Japan. J. Vet. Med. Sci. 73, 869–875. https://doi.org/10.1292/jvms.10-0208

O'Neill, D.G., Coulson, N.R., Church, D.B., Brodbelt, D.C., 2017. Demography and disorders of German Shepherd Dogs under primary veterinary care in the UK. Canine Genet. Epidemiol. 4, 7. https://doi.org/10.1186/s40575-017-0046-4

Parthasarathy, V., Crowell-Davis, S.L., 2006. Relationship between attachment to owners and separation anxiety in pet dogs (Canis lupus familiaris). J. Vet. Behav. Clin. Appl. Res. 1, 109–120. https://doi.org/10.1016/j.jveb.2006.09.005

Podberscek, A.L., Serpell, J.A., 1996. The English Cocker Spaniel: preliminary findings on aggressive behaviour. Appl. Anim. Behav. Sci. 1–2, 75–89. https://doi.org/10.1016/0168-1591(95)01012-2

Rehn, T., Keeling, L.J., 2011. The effect of time left alone at home on dog welfare. Appl. Anim. Behav. Sci. 129, 129–135. https://doi.org/10.1016/j.applanim.2010.11.015

Rooney, N., Bradshaw, J., 2014. Canine Welfare Science: An Antidote to Sentiment and Myth, in: Horowitz, A. (Ed.), Domestic Dog Cognition and Behavior. Springer Berlin Heidelberg, pp. 241–274. https://doi.org/10.1007/978-3-642-53994-7_11

Rooney, N.J., Cowan, S., 2011. Training methods and owner–dog interactions: Links with dog behaviour and learning ability. Appl. Anim. Behav. Sci. 132, 169–177. https://doi.org/10.1016/j.applanim.2011.03.007

Roth, L.S.V., Faresjö, Å., Theodorsson, E., Jensen, P., 2016. Hair cortisol varies with season and lifestyle and relates to human interactions in German shepherd dogs. Sci. Rep. 6. https://doi.org/10.1038/srep19631

Salman, M.D., Hutchison, J., Ruch-Gallie, R., Kogan, L., Jr, J.C.N., Kass, P.H., Scarlett, J.M., 2000. Behavioral Reasons for Relinquishment of Dogs and Cats to 12 Shelters. J. Appl. Anim. Welf. Sci. 3, 93–106. https://doi.org/10.1207/S15327604JAWS0302_2

Serpell, J.A., Duffy, D.L., 2016. Aspects of Juvenile and Adolescent Environment Predict Aggression and Fear in 12-Month-Old Guide Dogs. Front. Vet. Sci. 3. https://doi.org/10.3389/fvets.2016.00049

Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. 19, 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Svartberg, K., 2005. A comparison of behaviour in test and in everyday life: evidence of three consistent boldness-related personality traits in dogs. Appl. Anim. Behav. Sci. 91, 103–128. https://doi.org/10.1016/j.applanim.2004.08.030

Tiira, K., Lohi, H., 2015. Early Life Experiences and Exercise Associate with Canine Anxieties. PloS One 10, e0141907. https://doi.org/10.1371/journal.pone.0141907

Wiener, P., Haskell, M.J., 2016. Use of questionnaire-based data to assess dog personality. J. Vet. Behav. Clin. Appl. Res. 16, 81–85. https://doi.org/10.1016/j.jveb.2016.10.007

Wilsson, E., 2016. Nature and nurture - How different conditions affect the behavior of dogs. J. Vet. Behav. Clin. Appl. Res. 16, 45–52. https://doi.org/10.1016/j.jveb.2016.10.002

Wilsson, E., Sinn, D.L., 2012. Are there differences between behavioral measurement methods? A comparison of the predictive validity of two ratings methods in a working dog program. Appl. Anim. Behav. Sci. 141, 158–172. https://doi.org/10.1016/j.applanim.2012.08.012

Tables

Table 1 Statistics for scores in behaviour characteristics calculated for German Shepherd dogs (GSD_{Comp}) using a principal component analysis to condense the C-BARQ questions.

	N	Average	SD	Median	Min	Max	Range
Stranger-directed aggression	1033	0.00	0.99	-0.24	-1.81	6.67	8.48
Dog-directed aggression	906	0.01	1.03	-0.19	-2.41	3.32	5.73
Stranger-directed fear	1018	0.01	0.99	-0.13	-2.26	7.77	10.03
~~Playfulness~~Human-directed playfulness	1031	0.00	0.99	0.22	-4.96	1.89	6.84
Resource guarding	967	0.00	1.03	-0.16	-1.24	12.33	13.57
Excitability	1038	0.00	1.00	0.02	-3.12	2.60	5.71
Separation anxiety	1010	0.00	1.00	-0.32	-1.56	9.02	10.57
Lack of obedience	1011	-0.01	1.00	-0.10	-2.33	4.61	6.93
Stranger-directed interest	985	-0.01	1.01	0.03	-2.92	2.51	5.43
Attention seeking	1003	0.01	1.00	0.05	-3.17	3.31	6.48
Chasing	966	0.01	1.02	0.00	-2.60	2.93	5.54
Non-social fear	1025	0.00	0.98	-0.29	-2.30	5.58	7.88
Dog-directed fear	1001	0.02	1.00	-0.16	-4.10	5.18	9.28
Aversion being stepped over	1029	0.00	1.00	-0.08	-1.93	15.43	17.36
Touch-sensitivity	966	0.01	0.99	-0.26	-2.75	6.44	9.19

Table 2 Statistics for scores in general dog behaviour characteristics (Dog_{Comp}). Individual scores were calculated as an average over a set of C-BARQ questions defined in [1]Duffy & Serpell (2012) and [2]Svartberg (2005) and could range from 0 to 4.

	N	Average	SD	Median	Min	Max	Range	SE
Trainability[1]	1030	2.63	0.33	2.63	0.00	4.00	4.00	0.01
Stranger-directed aggression[1]	1033	0.45	0.52	0.30	0.00	4.00	4.00	0.02
Owner-directed aggression[1]	1020	0.08	0.23	0.00	0.00	2.75	2.75	0.01
Stranger-directed fear[1]	1003	0.15	0.40	0.00	0.00	4.00	4.00	0.01
Non-social fear[1]	1030	0.26	0.36	0.17	0.00	2.60	2.60	0.01
Dog-directed aggression[1]	1006	1.21	1.03	1.00	0.00	4.00	4.00	0.03
Dog-directed fear[1]	1001	0.41	0.70	0.00	0.00	4.00	4.00	0.02
Touch sensitivity[1]	953	0.26	0.39	0.00	0.00	3.00	3.00	0.01
Separation-related behaviours[1]	1025	0.20	0.35	0.00	0.00	2.75	2.75	0.01
Excitability[1]	1038	2.17	0.86	2.17	0.00	4.00	4.00	0.03
Attachment/ attention seeking[1]	1028	1.91	0.75	1.83	0.00	4.00	4.00	0.02
Chasing[1]	977	1.77	1.04	1.67	0.00	4.00	4.00	0.03
Energy level[1]	1028	2.32	0.99	2.50	0.00	4.00	4.00	0.03
Stranger-directed interest[2]	985	2.34	1.21	2.33	0.00	4.00	4.00	0.04
Human-directed playfulness ~~interest~~[2]	1031	3.15	0.71	3.20	0.00	4.00	4.00	0.02
Dog-directed interest[2]	961	2.01	1.04	2.00	0.00	4.00	4.00	0.03

630 Table 3 Effect sizes of demographic and management factors for the models that best predicts

631 the GSD behavioural traits

	PC1: Stranger-directed aggression	PC2: Dog-directed aggression	PC3: Stranger-directed fear	PC4: ~~Playfulness~~Human-directed playfulness	PC5: Resource guarding	PC6: Excitability	PC7: Separation anxiety	PC8: Lack of obedience	PC9: Stranger-directed interest	PC10: Attention seeking	PC11: Chasing	PC12: Non-social fear	PC13: Dog-directed fear	PC14: Aversion being stepped over	PC15: Touch-sensitivity
Cohort (UK vs Sweden)	**0.60**	**-0.35**		**-0.67**	0.14			**-0.28**	**0.68**	**-0.25**	**0.62**		**-0.27**		
People_hh								0.04						-0.04	-0.04
Children_hh															
Dogs_hh (yes)		**-0.30**			**-0.21**		**-0.14**	**-0.24**		-0.15			**0.15**		-0.12
Animals_hh (yes)			-0.24						0.13		**-0.30**				
Living place															
outdoors vs indoors				0.35		**-0.42**									
indoors/outdoors vs indoors				0.00		-0.28									
working place vs indoors				**-0.99**		-0.31									
Age[3]	-0.02	0.02	**-0.03**	**-0.07**	0.02				0.02		**-0.03**	-0.03	-0.02		
Gender															
Neuter status															
Gender*Neuter status															
Female neutered vs female intact			0.11	0.12			-0.13			0.00		0.16	-0.01	-0.08	
Male intact vs female intact			-0.03	**0.18**			0.12			**0.20**		0.07	**-0.19**	-0.07	
Male neutered vs female intact			**-0.20**	0.02			0.03			0.03		**0.40**	-0.01	**0.29**	
Coat colour															
Sable vs GSD coloured											**0.21**				
Black vs GSD coloured											0.09				
Other vs GSD coloured											-0.06				
Age.acquisation				**-0.04**					-0.04				-0.03		-0.03
Bred (yes)			-0.15								**-0.26**				
Shape	0.13										-0.15		**-0.23**		
Role_PC1	0.06						-0.05								
Role_PC2				-0.05								**0.06**			
Comp_PC1	**-0.09**													-0.06	**-0.08**
Comp_PC2	-0.05			**0.10**				-0.05				-0.05			
Commands		**0.05**		**0.08**				-0.04		**-0.09**	**0.04**	**-0.04**			**0.05**
Train_PC1														0.05	**-0.08**
Train_PC2															-0.07
Train_PC3		**-0.08**	**-0.06**		-0.07				**-0.07**					**-0.08**	
F_walking	**0.17**		**-0.11**				-0.14				0.11				
F_interaction_humans	**-0.14**								**0.07**						
F_interaction_dogs		**-0.16**		-0.04									-0.06		-0.05
F_training								**-0.10**	0.06		-0.06				
F_exercise					0.09		**0.12**			**0.16**					
F_offlead	-0.05				0.05	**0.07**	-0.05	**-0.12**		0.06	**-0.05**				
VarExp[1]	9.0	11.0	3.6	16.1	2.3	1.3	2.7	10.3	16.9	6.1	13.0	3.7	3.7	2.7	2.8

632 Significant effects ($p < 0.05$) are highlighted in bold

633 [1] Variance explained by the final model

Figure Captions

Figure 1 Effect display for the cohort in the generalised linear model fit for behaviour components. The fitted values for the cohort are shown for all behaviour components were this factor appeared in the final model with upper and lower confidence bounds.

Figure 2 Effect display for the dog's living place in the generalised linear model fit for behaviour components. The fitted values for the living place are shown for all behaviour components were this factor appeared in the final model with upper and lower confidence bounds.

Figure 3 Effect display for the interaction between sex and neuter status in the generalised linear model fit for behaviour components. The fitted values for the interaction between sex and neuter status are shown for all behaviour components were this factor appeared in the final model with upper and lower confidence bounds.

Figure 4 Effect display for the dog's coat colour in the generalised linear model fit for behaviour components. The fitted values for the coat colour are shown for all behaviour components were this factor appeared in the final model with upper and lower confidence bounds.

Supplement

Supplement 1 English version of the lifestyle survey

Supplement 2 Description of demographic and management factors assessed with the lifestyle survey that were used in the multivariate analyses. The distribution of factors is shown among the two cohorts "UK" and "Sweden".

Supplement 3 GSD_{Comp} generated by a principal component analysis of C-BARQ responses with the questions that loaded with $\geq |0.55|$ to the 15 components. The variance explained by the component is in parentheses after the component name.

Supplement 4 Correlation between demographic and management factors of German Shepherd dogs.