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Heritability of dominant–aggressive behaviour in English Cocker Spaniels

Joaquín Pérez-Guisado^{a,*}, Rocío Lopez-Rodríguez^a,
Andrés Muñoz-Serrano^b

^a*Departamento de Medicina y Cirugía Animal, Facultad de Veterinaria, Universidad de Córdoba,
Campus de Rabanales, 14071 Córdoba, Spain*

^b*Departamento de Genética, Facultad de Veterinaria, Universidad de Córdoba,
Campus de Rabanales, 14071 Córdoba, Spain*

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Abstract

A total of 51 seven-week-old English Cocker Spaniel puppies were measured for dominant–aggressive behaviour using the Campbell Test. The dogs consisted of a F_1 full sibs and half sibs from matings of 4 sires with 10 dams. The purpose of this study was to determine if the variability observed in this behavioural characteristic has an additive genetic component and if so, to estimate heritability (h^2). Coat colour and sex were examined as fixed effects.

According to the results of the study: (1) there are highly significant differences between sexes; with males being more dominant than females, regardless of coat colour; (2) there are highly significant differences in aggressive behaviour depending on coat colour with greater to lesser dominance found in golden, black and particolour coats in that order; (3) there is no interaction between sex and colour when exhibiting greater or lesser dominance; (4) heritability, estimated on sire components, is $h^2_S = 0.20$, indicating that the variability observed in dominant–aggressive behaviour is in part due to genetic factors; and (5) heritability estimated on dam components is $h^2_D = 0.46$, which implies that the maternal effect (genetic and environmental) is an important factor in this type of behaviour.

It is concluded that there is an additive genetic, and therefore, hereditary factor for dominant–aggressive behaviour in the English Cocker Spaniel. Some of the fixed factors include: sex (males are dominant over females), coat colour (golden-coated are the more dominant dogs followed by the

* Corresponding author. Tel.: +34 61 9883319; fax: +34 95 7212072.
E-mail address: pv1peguj@uco.es (J. Pérez-Guisado).

black-coated and finally by the particolour coat dogs) and the common environmental effect due to litter.

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1. Introduction

Canine aggression is an issue of special importance due to both frequency and potential consequences. More than 240 people are hospitalised each year in Holland for this reason (Shellart and den Hertog, 1998; Toet and Den Hertog, 2000), but also because it is one of the leading causes of euthanasia in dogs (Mikkelsen and Lund, 1999).

When examining the genetic basis for human aggression, several models have been employed using rodents (de Boer et al., 2003; Hogg et al., 2000; Palmour, 1983). However, we suggest that dogs could be a more valid model given that, like humans, their ancestors hunted in hierarchically structured groups (Overall, 2000) and hunting constitutes an aggressive behavioural pattern. Moreover, aggression is an expression of a biological function related to evolutionary reproductive success (Wilson and Daly, 1986) and a dominant trait that is more commonly found in males than in females (Cameron, 1997; Guy et al., 2001; Landsberg et al., 1998) as males must fight among themselves to defend both their territory and females against possible competitors. This aggressive behaviour is relevant because: the dominance is the most important cause of aggression diagnosed in dogs (Beaver, 1983), dominance aggression is a predominantly male trait (Line and Voith, 1986) and dogs with aggression's problems (toward owners and strangers) are more frequent in males than females (Takeuchi et al., 2001).

Aggressive behaviour is divided into different types of aggression according to the nature of the stimulus (Blackshaw, 1991; Borchelt, 1983; Popova et al., 1993). Thus, it can be defined as dominant aggression, territorial aggression, possessive aggression, protection of litter motivated aggression, pain motivated aggression, fear motivated aggression, predation aggression, play motivated aggression, redirected aggression, intra-specific aggression, idiopathic aggression, physiopathological and learned aggression (Landsberg et al., 1998).

All of these types of aggressive behaviours may be present to a greater or lesser degree in humans for purely physiological or adaptive reasons. While aggression is usually considered a normal behaviour as long as it does not constitute a threat to the individual's social group, it can also be a pathological disorder resulting from deviated adaptive processes in which basic social rules are not respected. In fact, approximately 1.6 million people die every year as a result of acts of violence. Violence is one of the leading causes of death in people aged 15–44, with more men (14%) than women (7%) committing aggression-related acts (Krug et al., 2002). Studies conducted in this line with adult dogs have confirmed that males are more dominant than females (Cameron, 1997; Guy et al., 2001; Landsberg et al., 1998), males show more aggression problems

than females and there are breeds with more aggression problems than others (Beaver, 1985; Lund et al., 1996; Takeuchi et al., 2001). It is well known that environmental factors have behavioural influences, moreover studies have found that skin characteristic can have behavioural relations (Smith and Gong, 1974; Grandin et al., 1995; Ortize de Zarate and Ortize de Zarate, 1991) and that single-coated English Cocker Spaniel (black or golden) are more aggressive than particolour individuals (Podberscek and Serpell, 1997).

As regards genetic influence, behavioural patterns have been associated with breed in dogs (James, 1951; Green and Woodruff, 1988; Bradshaw and Brown, 1990), and it has been suggested that high levels of aggression in mice have a genetic basis (Palmour, 1983). Hence there seems to be a general consensus that both genetic and environmental factors play a key role in the onset and exhibition of aggressive behaviour, particularly polygenic factors (Enserink, 2000; Tecott and Barondes, 1996).

The fact that at seven weeks old, the puppy's electroencefalogram is the same as at adulthood suggests that at seven weeks its genetic effect on aggression can be measured most clearly as there has been little effect of any socialization process (Hasbrouck, 1995). Although seven weeks is the age of maximum socialization (Vollmer, 1980), and the puppy is a dynamic organism whose behaviour is affected by its environment, its behavioural tendencies are predictable (Campbell, 1972). For this reason, we decided to evaluate dominance tendencies in seven weeks old dogs and we selected for our study the Campbell test among the available tests for this evaluation, as it is popular and widely used, because it is easy to do and gives quick results.

We have chosen the English Cocker Spaniel because is one of the breeds with greater problems of aggression toward humans (Beaver, 1983; Lund et al., 1996) and because it is a breed exhibiting different coat colours.

The purpose of this study, then, is to examine fixed and genetic random factors, in seven-week-old English Cocker Spaniel puppies using the Campbell Test (Campbell, 1972; Rossi, 1992; Hasbrouck, 1995; Velilla, 1998) in order to determine the following endpoints:

- (1) If differences in dominant behaviour between males and females are exhibited at the age of seven weeks.
- (2) If coat colour constitutes a fixed factor having an effect on dominantly aggressive behaviour in puppies.
- (3) If there is a hereditary basis for variability in dominant–aggressive behaviour in dogs and if so, to calculate heritability.

2. Material and methods

2.1. Description of test

The Campbell Test was conducted to assess dominant behaviour in puppies (Campbell, 1972; Rossi, 1992; Hasbrouck, 1995; Velilla, 1998). The test consists of five parts and must be conducted at the age of six to eight weeks old. Puppies are subjected to the test individually with no other person, animal or object present that could distract them. The

test leader (TL), not previously encountered by the puppy, should remain impassive and show no signs of emotion throughout the test. The five parts of the test include:

- (1) *Social attraction*: The puppy is placed at one end of the room (or in the centre of a particularly large room) facing the wall. TL quickly moves in the opposite direction away from the puppy, kneels down and claps his hands to gain the puppy's attention. Possible responses include: (a) the puppy comes readily, tail up, seeking contact with TL; (b) the puppy comes readily, tail down, makes no contact with TL; (c) the puppy comes readily, tail down; (d) the puppy comes hesitantly, tail down; (e) the puppy does not come or runs away.
- (2) *Following*: The puppy is placed at one end of the room at TL's feet. TL walks away in the opposite direction, making sure the puppy's attention is gained. Possible responses include: (a) the puppy follows TL readily at feet, tail up, trying to play; (b) the puppy follows TL readily at feet, tail up; (c) the puppy follows TL readily, tail down; (d) the puppy follows hesitantly; (e) the puppy does not follow or runs away.
- (3) *Restraint*: TL places the puppy on its back on the floor, holding the puppy down with one hand on its chest. Possible responses include: (a) the puppy struggles vigorously, biting or growling, tail wagging; (b) the puppy struggles vigorously, tail wagging, no biting or growling; (c) the puppy struggles, then calms down; (d) the puppy does not struggle and may lick TL's hands.
- (4) *Social dominance*: TL holds the puppy gently around the neck with one hand while stroking backward along its neck and back for 30 s. Possible responses include: (a) the puppy rebels, growls and/or tries to bite; (b) the puppy rebels but does not exhibit aggressive behaviour; (c) the puppy rebels for only a short period of time; (d) the puppy adopts supine position; (e) the puppy walks away and does not return.
- (5) *Elevation dominance*: TL picks up the puppy, holding it around its chest (TL places hands between hind legs) a short distance above the floor. Possible responses include: (a) the puppy struggles vigorously, growls and/or tries to bite; (b) the puppy struggles vigorously but does not exhibit aggressive behaviour; (c) the puppy struggles, calms down and/or licks TL's hands; (d) the puppy does not struggle and may lick TL's hands.

The scores on the different parts of the test indicate: (a) excessive dominance; (b) dominance; (c) balanced submission; (d) excessive submission; (e) independence or deficient socialisation. Responses on the test indicate the degree of dominance exhibited by the puppy with maximum dominance corresponding to (a), dominance to (b), balanced submission to (c), excessive submission to (d) and independence or excessive fear to (e).

2.2. Study sample

A total of 51 seven-week-old English Cocker Spaniel puppies (28 males and 23 females) were subjected to the Campbell Test. The test was always carried out by the same person (male sex) and the puppies were not weaned and came from litters that lived with their owners together. All the puppies came from the first litter of their mothers. The tests were conducted on 10 litters from matings as shown in [Table 1](#). Therefore, we used matings that had already been made.

Table 1
Distribution of colours for the different matings performed of 4 sires and 10 dams from different breeders

Sires	Dams	Progeny
Particolour	Golden	4 Golden
	Black	6 Black
	Particolour	5 Particolour
Golden	Golden	5 Golden
	Black	5 Black
Black	Golden	6 Black
	Black	4 Black
Black	Golden	2 Black, 3 Golden
	Golden	2 Black, 3 Golden, 1 Particolour
	Black	3 Black, 1 Golden, 1 Particolour

Matings of 4 sires and 10 dams from different breeders.

2.3. Statistical analyses

Statistical analyses were made using a variable which consisted of the mean puppy test score as calculated from the scores on each of the five parts of the test. Higher mean scores indicated greater dominance, while lower mean scores indicated submission. This variable ranged from 0.0 to 4.0, with 40 possible values.

Fixed effects were estimated using Type III sums of squares in the SAS software GLM procedure (SAS Institute Inc., 1992) with the following model:

$$X_{ijklm} = \mu + S_i + C_j + (S \times C)_{ij} + e_{ijk}$$

where X_{ijklm} is the total score for each individual; S_i the 'sex' effect (i = male and female); C_j the 'coat colour' effect (j = black, golden and particolour); $(S \times C)_{ij}$ is the 'sex-coat colour interaction' effect.

Duncan's Test was also conducted to examine the magnitude and significance of the mean effects of both sex and coat colour.

The observational components of variance were estimated using the SAS software VARCOMP (MIVQUEO option) procedure (SAS Institute Inc., 1992) with the following model:

$$X_{ijklm} = \mu + S_i + C_j + (S \times C)_{ij} + S_k + D_{l(k)} + e_{ijklm}$$

where the first three terms of the model are fixed effects and where X_{ijklm} is the total score for each individual; S_i the 'sex' effect (i = male and female); C_j the 'coat colour' effect (j = black, golden and particolour); $(S \times C)_{ij}$ the 'sex-coat colour interaction' effect; S_k the k th sire effect; $D_{l(k)}$ the l th dam effect in the k th sire; e_{ijklm} is the individual variability of the progeny.

The MIVQUEO option produces unbiased estimates that are invariant with respect to the fixed effects of the model and are locally best quadratic unbiased estimates given that the true ratio of each component to the residual error component is zero.

Estimations of the components of genetic variance are as follows (Falconer and Mackay, 1995):

$$\begin{aligned}\sigma_S^2 &= \text{Cov}_{\text{HS}} = \frac{1}{4}\tilde{\sigma}_A^2 \\ \sigma_D^2 &= \text{Cov}_{\text{FS}} - \text{Cov}_{\text{HS}} = \frac{1}{2}\tilde{\sigma}_A^2 + \frac{1}{4}\tilde{\sigma}_D^2 - \frac{1}{4}\tilde{\sigma}_A^2 = \frac{1}{4}\tilde{\sigma}_A^2 + \frac{1}{4}\tilde{\sigma}_D^2 + \tilde{\sigma}_{\text{EC}}^2 \\ \sigma_W^2 &= \sigma_P^2 - \text{Cov}_{\text{FS}} = \frac{1}{2}\tilde{\sigma}_A^2 + \frac{3}{4}\tilde{\sigma}_D^2 + \tilde{\sigma}_{\text{EW}}^2 \\ \sigma_T^2 &= \sigma_S^2 + \sigma_D^2 + \sigma_W^2 = \tilde{\sigma}_A^2 + \tilde{\sigma}_D^2 + \tilde{\sigma}_{\text{EC}}^2 + \tilde{\sigma}_{\text{EW}}^2 \\ h_S^2 &= \frac{4\sigma_S^2}{\sigma_T^2} = \frac{\tilde{\sigma}_A^2}{\tilde{\sigma}_P^2} = h^2 \\ h_D^2 &= \frac{4\sigma_D^2}{\sigma_T^2} = \frac{\tilde{\sigma}_A^2 + \tilde{\sigma}_D^2 + 4\tilde{\sigma}_{\text{EC}}^2}{\tilde{\sigma}_P^2} = h^2 + \frac{\tilde{\sigma}_D^2 + 4\tilde{\sigma}_{\text{EC}}^2}{\tilde{\sigma}_P^2}\end{aligned}$$

where σ_S^2 and σ_D^2 are the observational variances due to sires and dams, respectively; σ_W^2 the observational within progeny component of variance; σ_T^2 the observational total phenotypic variance; Cov_{HS} and Cov_{FS} the half and full sibs covariances, respectively; $\tilde{\sigma}_A^2$ and $\tilde{\sigma}_D^2$ the causal additive and dominant variances; $\tilde{\sigma}_{\text{EC}}^2$ the causal variance due to a common environment; $\tilde{\sigma}_{\text{EW}}^2$ is the causal within-group component of variance.

3. Results and discussion

3.1. Effect of sex on behaviour

Table 2 shows the mean values and standard errors of the effects for sex on behaviour. As confirmed by other studies with adult dogs (Cameron, 1997; Guy et al., 2001; Landsberg et al., 1998), males were observed to have a higher mean than females. The effect of sex on dominance behaviour was found to be independent of coat colour, that is, there was no interaction between sex and colour. This suggests that males exhibit more dominant behavioural characteristics than females, regardless of coat colour. Duncan's Test gave two significantly different groups: males, with a mean value of 2.80000 and females, with a mean value of 2.02609.

3.2. Effect of coat colour on behaviour

In coat colour, the solid colour is genetically dominant over particolour. Within solid colour, black is dominant over golden colour. Table 3 shows the means and standard errors

Table 2
Effect of sex on behaviour \pm standard errors

Sex	Mean	Significance ^a
Sire	2.800 \pm 0.057	A
Dam	2.026 \pm 0.038	B

^a Different letters (A and B) are means significantly different, $p < 0.001$.

Table 3
Effect of coat colour on behaviour ± standard errors

Coat colour	Mean	Significance ^a
Golden	2.675 ± 0.119	A
Black	2.407 ± 0.081	B
Particolour	2.114 ± 0.130	C

^a Different letters (A and B) are means significantly different, $p < 0.001$.

of the effects for coat colour. Duncan’s Test showed that each of the three coat colours included in the study had a significantly different effect on behaviour. Thus, golden, black and particolour coats, in that order, corresponded to greater or lesser dominant behavioural patterns. Our findings are in line with previous studies (Podberscek and Serpell, 1996) which have demonstrated that aggressive behaviour, including dominance aggression (8 of the 13 situations evaluated were a result of dominance aggression) is associated with coat colour in a great many situations. These authors have found that dogs with golden, black and particolour coats exhibit decreasingly aggressive behaviour.

3.3. Interaction between sex and colour

No interaction was found between these two factors. Regardless of their colour, males were found to be more dominant than females.

3.4. Heritability of dominant–aggressive behaviour

Similar to previous studies which have found an association between behavioural patterns and breed (Green and Woodruff, 1988; Bradshaw and Brown, 1990) and high levels of aggression and genetic factors in mice (Palmour, 1983), we obtained significant values when studying the causal components of variance in dominant behaviour. As shown in Table 4, the heritability value is 0.20, meaning that additive variance constitutes 20% of phenotypic variance. Maternal effects were also observed as demonstrated by the fact that the estimated heritability from dams (h_D^2) is more than twice that of the estimate heritability from sires (h_S^2).

Table 4
Observational component of variance in a half-sib and full-sib analysis

Sources	Variance	Causal components estimated
Sires (σ_S^2)	0.00169190	$\frac{1}{4}\sigma_A^2$
Dams (σ_D^2)	0.00389376	$\frac{1}{4}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \sigma_{EC}^2$
Progeny (σ_W^2)	0.02834603	$\frac{1}{2}\sigma_A^2 + \frac{3}{4}\sigma_D^2 + \sigma_{EW}^2$
Total (σ_T^2)	0.0339317	σ_P^2

$$\sigma_A^2 = 4\sigma_S^2 = 0.0068; \sigma_D^2 - \sigma_S^2 = \frac{1}{4}\sigma_D^2 + \sigma_{EC}^2 = 0.0022; \sigma_W^2 - 2\sigma_S^2 = \frac{1}{4}\sigma_D^2 + \sigma_{EW}^2 = 0.0250; h_S^2 = \frac{0.0068}{0.0339} =$$

$$0.20 = h^2; h_D^2 = \frac{0.0156}{0.0339} = 0.46 = h^2 + \frac{\sigma_D^2 + 4\sigma_{EC}^2}{\sigma_P^2}.$$

4. Conclusions

Our findings suggest that in the English Cocker Spaniel and according to dominance criterion Campbell test: (a) dominant behaviour is greater in males than in females and is already exhibited in puppies; (b) the fixed factor coat colour has a significant influence on dominant behaviour with golden, black and particolour coats ranked from most to least dominant in that order; (c) there is no interaction between sex and colour: males are more likely to exhibit dominant behaviour than females, regardless of coat colour; (d) dominant behaviour is a heritable trait with a heritability of 20%. Finally, there is a significant maternal effect.

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