4 Genetic aspects of dog behaviour with particular reference to working ability

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Introduction

Anyone using dogs as working animals has an obvious interest in knowing: (a) the degree to which specific features are inherited; (b) the magnitude of the differences which exist between breeds; and (c) the relationship, if any, between specific traits. Although the dog has had a longer association, and enjoys closer contacts, with humans than any other species, genetic studies on the domestic dog are not extensive. Most genetic work has been directed towards understanding the mode of inheritance of specific physical anomalies, whereas advanced studies on the inheritance of behaviour are relatively recent and stem largely from the pioneering work that led to the publication of Scott & Fuller (1965). Mackenzie, Oltenacu & Houpt (1986) provided a broad review of behaviour genetics of the dog, but the present review focuses specifically on the genetics of working behaviour, since it is in this field that behaviour studies are likely to have the greatest practical impact.

Background

As Mackenzie *et al.* (1986) have shown, studies on the inheritance of behaviour began around the turn of the century, but much of the early work was confined to well-established traits with a clear intention of finding Mendelian explanations. Thus we see Whitney (1929*b*) suggesting that, in foxhounds, vocal trailing is dominant to mute trailing. Similarly, Humphrey & Warner (1934) suggested that gunshyness in German Shepherd dogs (GSDs) was controlled by a simple gene series with two alleles: N causing under-sensitivity, and n causing over sensitivity. Thus NN animals were largely insensitive to sound, Nn were medium sensitive and nn oversensitive. In addition to auditory sensitivity, these workers also looked at sensitivity to touch and postulated a similar theory with SS being undersensitive, Ss medium sensitive and ss oversensitive. They considered that ss and nn animals were too sensitive to train effectively, and that the best animals to train were Nn/Ss. While most trainers would agree with the difficulties experienced in trying to train over or undersensitive animals, it is highly unlikely that such complex features as ear and body sensitivity are going to be inherited as simple Mendelian traits. Not only will such sensitivities be influenced by complex genetic factors, they will also be modified through interactions with the environment.

Humphrey & Warner (1934) calculated phenotypic correlations among 42 physical and 9 behavioural traits in GSDs, and found that 15 of the 378 possible correlations reached statistical significance. It is probable that the underlying genetic correlations were quite different and that the project was oversimplified in seeking Mendelian explanations. Nevertheless, the Fortunate Fields study (Humphrey & Warner, 1934) did achieve success in producing superior animals for guide dog/police work using this simplified system.

The present paper looks at behaviour in guide dogs, hunting dogs, livestock guarding dogs and police/service dogs. The importance to man of herding dogs is without question, but so few genetic data exist in this field that herding dogs are deliberately excluded from the present discussion.

Guide dogs for the blind

The role of the guide dog must rank as one of the most useful modern occupations for a working dog. For a long time the GSD was the breed of choice, but in more recent years Labrador and golden retrievers, and their crosses, have been commonly used (male GSDs being slightly too large for the task). Many guide dog organizations now breed their own stock (that in Britain being the largest dog owning body in the country), and studies from these organizations are now coming to fruition.

Most guide dog failures arise from character faults, particularly fearfulness (Scott & Bielfelt, 1976; Goddard & Beilharz, 1982). Clear sex differences have also been noted: females, for example, show more suspicion and fearfulness, while males show more initiative. When assessing the degree to which a character or trait might be inherited an important consideration is its heritability. Strictly, heritability is the proportion of the total variance observed in a trait that is due to additive effects. In lay terms, it might be best defined as that proportion of the parental superiority (over the population average) which is transmitted to the offspring. Thus, a heritability of 40% would suggest that only 40% of any parental superiority (or inferiority) would be passed on to the progeny. Heritability studies are usually based upon paternal half-sib correlations, i.e. correlations

Table 4.1. *Heritability estimates for guide dog traits (Australia)*

Trait	Sire		Dam		Combined	
	h^2	SE	h^2	SE	h^2	SE
Success	0.46	0.19	0.42	0.18	0.44	0.13
Fear	0.67	0.22	0.25	0.15	0.46	0.13
Dog distraction	–0.04	0.08	0.23	0.14	0.09	0.08
Excitability	0.00	0.09	0.17	0.13	0.09	0.08

Source: Goddard & Beilharz (1982).

between the performances of different progeny sired by a particular father. For such studies a series of sires needs to be used but the performance of the sire is not required, only that of his progeny. Alternatively, offspring–parent regressions can be made, in which case the performance of both offspring and parents needs to be known. These offspring–parent regressions can be based upon one parent (usually the sire) or the average of both parents (termed offspring–mid-parent regressions). A difficulty with such methods is that parents and offspring are, of necessity, assessed in different years, even if assessed at comparable ages.

Heritability studies are, strictly speaking, only relevant to the population from which they were derived and for the period of time when they were assessed. Nevertheless, they can provide a broad guide to inheritance. Because heritabilities are ratios they are susceptible to variation caused by environmental features. Failure to reduce environmental variation or to assess animals in a consistent fashion will tend to reduce heritability estimates and thus produce values that may be lower than the true figures. Despite these limitations, heritabilities are important because they give guidelines to the consequences of various selection procedures. Highly heritable traits should respond well to direct selection and performance testing, whereas low values may necessitate selection through progeny, or even the use of crossbreeding, to produce genetic advances.

Heritability estimates derived from 394 Australian guide dogs (Labrador retrievers) are shown in Table 4.1. They were generally high for 'success at becoming a guide dog' and for 'fear' (the principal cause of culling) (Goddard & Beilharz, 1982). Heritability estimates from American guide dogs (various breeds), based on over 700 males and over 1000 females, were produced by Bartlett (1976) and are given in Table 4.2. In many cases values did not differ significantly from zero, but some aspects of sensitivity were moderately heritable. Studies on Californian guide dogs (mainly GSD) have been published by Scott & Biefelt (1976) and are shown in Table 4.3. In 11 of the 13 traits, dam components attained higher heritabilities than sire components emphasizing the importance of maternal effects. However, most of the heritabilities were not significantly different from zero.

Both American studies suggest lower heritabilities for major traits than do the more recent Australian studies, but the reasons for this are unclear. The Australian figures derive from more sophisticated statistical analyses than the American ones, but one cannot

Table 4.2. *Heritability estimates for guide dog traits (USA)*

Trait	Male	Female	Both
Body sensitivity†	0.26	0.05	0.10
Ear sensitivity†	0.49	0.14	0.25
Fighting instinct†	–0.05	–0.08	–0.04
Protective instinct†	–0.21	–0.13	–0.12
Nose acuity††	0.30	0.05	0.12
Intelligence††	–0.17	–0.07	–0.06
Willingness††	–0.14	–0.04	–0.03
Energy††	–0.03	0.06	0.05
Confidence††	0.04	0.26	0.16
Self right†††	0.15	0.25	0.22

† low score least effect; †† low score greatest effect; ††† low score indicates most eager to submit to another.
Source: Barlett (1976)

Table 4.3. *Heritability estimates for guide dog traits (California)*

Trait	Feature	h^2
Sit	Forced sit with 3 repetitions	0.06
Come	Called with 5 repetitions	0.14
Fetch	Playful retrieving 3 repetitions	0.24
Trained response	Complex excitability, nervousness	0.08
Willingness	Responsiveness to tester	0.12
Body sensitivity	Complex reaction to pain	0.16
Ear sensitivity	Complex reaction to sound	0.00
New experience	Response to novel stimuli	0.06
Traffic	Reaction to moving cart	0.12
Footing crossing	Ability to identify surface underfoot	0.06
Closeness	How close passed to obstructions	0.04
Heel	Acceptance of leash training	0.10

Source: Scott & Bielfelt (1976)

exclude the possibility that American selection has gone on much longer and that this has resulted in the reduction in heritability estimates. It is also possible that the method of 'scoring' traits leads to marked differences in heritability estimates.

Genetic correlations between traits have been produced by Goddard & Beilharz (1983) for their Australian Labradors and by Bartlett (1976) for his American dogs. These are shown in Tables 4.4 and 4.5. The Australian work suggests high heritabilities for fear or 'nervousness', and strong positive correlations between this and 'sound shyness' and negative correlations with 'willingness'. Most practical breeders believe nervousness to be relatively strongly inherited, and there is empirical evidence in many breeds that breeding from nervous dogs leads to the production of increased proportions of nervous progeny (see below and Serpell & Jagoe, Chapter 6).

Hunting

Considering that man probably first used the dog as an aid to hunting (see Clutton-Brock, 1984 and Chapter 2), we have learned very little about hunting attributes in genetic terms. Whitney's (1929*a*, *b*) early work on hunting traits was largely confined to relatively simple behavioural features, whereas crossbreeding work by Marchlewski (cited in Burns & Frazer, 1966) showed that pointing behaviour was a complex trait with no indication that the progeny of superior field-trialists were any better than average. Sacher (1970) also showed that pointers' performance scores in field trials (on a 4-point system) were not normally distributed and that genetic influences could not be identified. Geiger (1972), working with German wirehaired pointers and a 12-point system, assessed 1463 progeny from 21 sires on four traits and obtained relatively high maternally derived heritabilities. However, he obtained insignificant sire values (Table 4.6) and no sex effects.

More recently, attempts have been made to examine the genetics of hunting potential in specific breeds in Scandinavia. Some of the principles involved in

Table 4.4. *Genetic correlations (below diagonal) and heritabilities (diagonal) in Labradors*

Trait	N	S	C	W	D	SS	B
Nervousness (N)	0.58						
Suspicion (S)	0.53	0.10					
Concentration (C)	−0.01	−0.31	0.28				
Willingness (W)	−0.57	−0.20	0.67	0.22			
Dog distraction (D)	0.11	0.63	−0.47	−0.41	0.08		
Sound-shy (SS)	0.89	0.47	0.33	−0.78	0.28	0.14	
Body sensitivity (B)	0.72	0.51	−0.29	−0.74	−0.21	0.59	0.33

Source: Goddard & Beilharz (1983).

Table 4.5. *Genetic correlations among temperament traits in American guide dogs*

Trait	BS	ES	OA	E	SR
Body sensitivity (BS)					
Ear sensitivity (ES)	1.00				
Olfactory acuity (OA)	0.75	0.58			
Energy (E)	–0.38	–0.77	–0.14		
Self-right (SR)	–0.15	–0.13	0.12	–0.14	
Confidence (C)	1.32	0.60	0.34	–0.04	–0.74

Source: Bartlett (1976).

Table 4.6. *Heritability estimates in German wirehaired pointers*

Trait	Sire	Dam
Hare tracking	0.03	0.46
Nose	0.01	0.39
Obedience	0.01	0.19
Seek	0.00	0.41

Source: Geiger (1972).

using tests as a basis for breeding work have been reviewed by Swenson (1987) and Vangen & Klemetsdal (1988). The latter looked at the English setter and Finnish spitz, both of which are used for hunting in Scandinavia more than they are in other countries. Heritabilities were calculated for various traits, as well as phenotypic and genetic correlations between traits. The researchers used 5285 English setter tests from 968 dogs by 224 sires, and 4864 Finnish spitz tests from 736 dogs by 212 sires. The results are shown in Tables 4.7 and 4.8.

Heritability estimates for English setter traits tended to be higher than those for those of Finnish spitz, but the authors emphasize that some traits did not show a normal distribution. For future work, they suggest that some traits be assessed as all-or-nothing, that identification by an experienced judge would be desirable and that adjustments for dog age are necessary (Vangen & Klemetsdal, 1988). For the Finnish spitz, breeding values[1] were calculated from the traits TS, HB and TI, and genetic progress[2] per year was shown to be +0.04%, –0.3% and +0.03% of the average score for the three traits, respectively. Vangen & Klemetsdal (1988) also recommended progeny testing, and they illustrated progeny test data for total scores that ranged from +7.83 to –4.26 but were based on too few progeny per sire to be meaningful.

Nevertheless the indications were that hunting traits were heritable, and that better systems of assessing such traits might lead to higher heritability figures and hence greater potential progress in selection. At present, failure to 'score' hunting traits accurately probably leads to lower estimates of heritability than may actually be the case. This will also lead to less accurate selection of breeding stock and hence reduced progress in hunting prowess.

Livestock guarding

In Central Europe, where the wolf survived longer than in places such as Britain, several large dog breeds evolved, which were intended to protect sheep flocks from predators and which were usually, though not exclusively, white in colour. In relatively recent times the effectiveness of such dogs as livestock protectors has been studied, primarily in USA. The first trials were conducted by Linhart *et al.* (1979), since which time it has been established that these dogs *can* deter coyote predation on sheep

[1] Breeding values for a sire can be defined as that sire's superiority over his contemporaries multiplied by the heritability of the trait being considered.

[2] Genetic progress is a measure of the advance in genetic quality that has occurred due to selection. Typically, it will be lower than the total improvement in quality, some of which will be due to environmental effects and/or training advances.

Table 4.7. *Genetic (above diagonal) and phenotypic (below diagonal) correlations together with heritabilities (diagonal) for English setters*

Trait	HE	SS	FW	CO	SI
Hunting eagerness (HE)	0.22	0.79	0.72	0.33	0.72
Style and speed (SS)	0.94	0.18	0.68	0.31	0.67
Field work (FW)	0.97	0.92	0.18	0.44	0.74
Cooperation (CO)	0.41	0.43	0.52	0.09	0.72
Selection index (SI)	0.80	0.74	0.64	0.61	0.17

Source: Vangen & Klemetsdal (1988).

Table 4.8. *Genetic (above diagonal) and phenotypic (below diagonal) correlations together with heritabilities (diagonal) for Finnish spitz*

Trait	TS	SA	FB	MK	BK	HB	FO	TI
Total score (TS)	0.11	0.48	0.51	0.57	0.48	0.66	0.60	0.72
Searching ability (SA)	0.61	0.07	0.15	0.30	0.35	0.22	0.48	0.43
Finding birds (FB)	0.94	0.79	0.11	0.13	0.10	0.17	0.16	0.28
Marking (MK)	0.77	0.97	1.00	0.04	0.48	0.35	0.33	0.47
Barking (BK)	0.46	–0.77	1.00	1.00	0.02	0.30	0.31	0.42
Holding birds (HB)	0.77	–0.01	0.31	0.55	–0.38	0.18	0.22	0.47
Following birds (FO)	0.59	1.00	0.55	0.37	–0.26	0.03	0.10	0.50
Total impression (TI)	0.83	–0.05	0.50	0.50	–0.14	1.00	0.13	0.09

Source: Vangen & Klemetsdal (1988).

(Green & Woodruff, 1983*a*, *b*). Ample evidence from questionnaires distributed to 399 livestock producers (763 dogs) demonstrated that these dogs were an economic asset: 71% of respondents suggested that their dogs were very effective, 21% somewhat effective and only 8% not effective (Green & Woodruff, 1988). Similar degrees of effectiveness have been reported by others (see review in Green & Woodruff, 1987). Bearing in mind the variable sources of the dogs and the differing environments to which they were exposed it is encouraging that they were successful at all.

In this area of behaviour there have been several studies on how livestock guarding dogs (LGDs) should be raised and trained (Coppinger *et al.*, 1983; Green & Woodruff, 1983*c*; McGrew & Andelt, 1985; Lorenz & Coppinger, 1986; see also Coppinger & Schneider, Chapter 3). Most studies involve raising LGDs with lambs from about eight weeks of age to encourage bonding, although the breeds studied have usually been those selected for this guarding trait. It has been argued that, over a long time, such breeds have been selected to show little or no predator behaviour at all (Coppinger, Smith & Miller, 1985), whereas herding breeds like the Border collie or kelpie have been selected to truncate the natural predatory sequence (see Coppinger & Schneider, Chapter 3). Breber (1977), however, has suggested that Maremmas only exhibit this loss of predatory behaviour if properly socialized to the sheep they guard, and only then if adequately fed. Coppinger *et al.* (1985) suggest that some mongrels may possess disrupted, missing or rearranged elements of the predatory sequence.

Bond-forming is well established in the dog (Scott & Fuller, 1965; Fox, 1978; Serpell & Jagoe, Chapter 6) and perhaps better exemplified in this species than in any other. It is argued that, because of the disruption of co-selected traits, mongrel dogs may be less likely to bond with alien species and be less protective of them than the Eurasian breeds selected for this affinity (Black, 1987). At the same

Table 4.9. *Comparison of five breeds of livestock guarding dog*

Breed[a]	No.	Effectiveness (%):			Aggression (%) to:	
		very	some	not	predators	dogs
Great Pyrenees	437	71	22	7	95	67
Komondor	138	69	1	12	94	77
Akbash	62	69	22	9	100	92
Anatolian	56	77	13	10	96	86
Maremma	20	70	20	10	94	94

[a] Other breeds omitted.
Source: Green & Woodruff (1988).

time, the smaller size of mongrels may prove less of a deterrent to predators. In contrast, Eurasian dogs are more trustworthy and large enough to deter many predators, although difficult and costly to obtain, and big enough to be a potential threat to humans.

Some studies on breed suitability have been hampered by lack of numbers. In their questionnaire study, Green & Woodruff (1988) looked at a variety of breeds but had sufficient numbers to compare only five. Their findings are shown in Table 4.9. Rates of success among the five breeds were not significantly different, although more komondors bit people than did Great Pyrenees, akbash or Anatolians. Similarly, fewer Great Pyrenees injured sheep than did komondors, akbash or Anatolians. It was observed that dogs reared with livestock from eight weeks or younger ($N = 280$) were more successful than dogs placed with livestock after eight weeks ($N = 227$), suggesting that bonding was easier prior to eight weeks of age.

A later study by Green (1989) used 100 purchased dogs placed with livestock breeders and showed a higher rating for Great Pyrenees than Anatolians. However, 40% of dogs injured livestock and 15% killed them. Significantly, more Anatolians than Great Pyrenees were involved in such attacks.

Recent data from Coppinger *et al.* (1988) were based on a ten-year study covering over 1000 dogs and using the co-operator questionnaire system. Using three purebreeds and two F1 crossbreeds they showed dogs to be effective at reducing predation. Average predation reduction was 64% with 53% of respondents claiming that predation was eliminated entirely. Although reluctant to claim breed differences, on the ground that their dogs represented strains within breeds rather than breeds *per se*, the authors did demonstrate differences between breeds. In two years of the study, breed differences reached significance and in the traits 'attentiveness' and 'trustworthiness' Maremmas and F1 Maremma/Šarplaninac crosses scored better than either Anatolians, Šarplaninac or F1 Anatolian/Šarplaninac. Even if these represented strain rather than breed differences, they do show that real differences exist which could be exploited.

Table 4.10. *Ratings of livestock guarding dogs (%)*

Breed[a]	Number	Good	Fair	Poor
Great Pyrenees	59	83	8	9
Anatolian	26	38	27	35

[a] other breeds deleted
Source: Green (1989)

LGDs are clearly successful at protection work, and Coppinger *et al.* (1988) have argued that, in some areas, guarding dogs are essential for livestock farmers to remain in business. However, the underlying genetic basis for the behaviour needs further study to clarify the degree to which livestock protecting behaviour is inherited, and to further document breed differences and examine the extent to which selection could give greater success. It is not yet known the extent to which good LGDs transmit their superiority to their progeny. If this is high, then selection for superior protection dogs could prove as effective as the selection of superior guide dogs.

Police/armed service work

Studies at the Swedish army centre of Solleftea have undertaken temperament tests on German shepherd dogs at around 18 months of age, following a period of 'puppy walking' in private homes. Reuterwall & Ryman (1973) have shown that the proportion of additive genetic variance is quite small for all the temperament traits tested. Heritability estimates derived from their components of variance values were produced by Willis (1976) and are shown in Table 4.11. Only three values reach significance, although the total sample size (488 males and 438 females) is certainly adequate.

These disappointingly low values suggest a very low additive effect on these traits. However, as Mackenzie *et al.* (1986) suggest, the scoring system used was perhaps too complex, and assessments made at 18 months may not provide a true reflection of inherited differences. The effects of early experience may be important, particularly since dogs would have been 'walked' in very different situations and would have experienced varying environments (see Serpell & Jagoe, Chapter 6).

More encouraging values for inherited traits in army dogs have been produced by Falt, Swenson & Wilsson (1982, cited by Mackenzie *et al.*, 1986). These were based upon tests undertaken on eight-week-old GSD puppies and are given in Table 4.12.

Most dog trainers would agree that pursuing and picking up an object is easier for a dog to achieve than actually returning with that object. The heritability estimates obtained by Falt *et al.* (1982) tend to confirm this genetically. It is necessary, however, to know the degree to which early testing at eight weeks of age can accurately identify adult behaviour patterns. In genetic work early identification is desirable, but canine behaviour is constantly changing in early life and early selection must be highly correlated with adult performance if such selection is to be useful.

The Schutzhund working degree is widely used in Germany and elsewhere as the basis for testing and selecting working breeds of dog. Schutzhund is particularly associated with German shepherd dogs since, without a Schutzhund qualification, GSDs cannot be exhibited as adults.

Table 4.11. *Heritabilities (half-sib) of mental traits in GSDs*

Trait	Paternal half-sib values	
	males	females
Affability	0.17	0.09
Disposition for self-defence	–0.11	0.26**
Disposition for self-defence and defence of handler	0.04	0.16
Fighting disposition	0.16*	0.21*
Courage	0.05	0.13
Ability to meet sudden strong auditory disturbance	–0.04	0.15
Disposition for forgetting unpleasant incidents	0.10	0.17
Adaptiveness to different situations	0.00	0.04

$^{*}P < 0.05$; $^{**}P < 0.01$.

Source: Willis (1976) after Reuterwall & Ryman (1973).

Schutzhund comes in three degrees termed SchH I, SchH II and SchH III with increasing number associated with increasingly advanced tests. Essentially, the tests are divided into four broad components which might be termed: tracking, obedience, man-work (protection) and character (courage). Several thousand tests are undertaken in Germany each year, and Schutzhund groups have been set up in the USA, Britain and Eire. Despite the effort expended on such testing, little genetic work has appeared. Pfleiderer-Hogner (1979) analysed the SchH I results from 2046 tests on 1291 GSDs from 37 different sires, all the testees being born in 1973. She found no effect of dog age at test or month of trial, but she did find significant effects of sex and of the number of competitors in a test. Heritability values derived from sire and dam components and combined estimates are given in Table 4.13. None of the values reach significance.

Phenotypic correlations between the different features are shown in Table 4.14. Three of these (starred) were significant, that between man-work and character being the highest.

Table 4.12. *Heritability estimates for 8-week-old traits in GSDs*

Trait	Feature	Sire	Dam
Yelp	Time from first separation to yelp	0.66	0.73
Shriek	Time for serious cry of distress	0.22	0.71
Contact 1	Approach to stranger in strange place	0.77	1.01
Fetch	Pursue and pick up ball	0.73	0.10
Retrieve	Bring back ball	0.19	0.51
Reaction	To strange object in strange place	0.09	1.06
Social competition	Tug-of-war	0.11	0.76
Activity	Exploration in strange arena	0.43	0.76
Contact 2	Time spent near stranger	0.05	1.11
Exploration	Visits to strange objects in arena	0.31	0.83

Source: Falt *et al.* (1982). Values in excess of 1.00 are not strictly possible and will have resulted from insufficient numbers or will have high standard errors attached to them.

Table 4.13. *Heritability estimates for SchH I scores*

Trait	Sire	Dam	Combined
Tracking	0.01	0.20	0.10
Obedience	0.04	0.13	0.09
Man-work	0.04	0.07	0.06
Character	0.05	0.17	0.12

Source: Pfleiderer-Hogner (1979).

Table 4.14. *Phenotypic correlations between Schutzhund traits*

Trait	TR	OB	MW
Tracking (TR)			
Obedience (OB)	0.26**		
Man-work (MW)	0.11	0.20*	
Character (CH)	0.10	0.17	0.76***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Despite these findings, it is difficult to accept that Schutzhund testing is genetically a waste of time and one has to conclude that, if these traits have a genetic basis, either they are controlled by non-additive factors (i.e. interactions between genes) or the flaws in testing are sufficiently serious as to prevent statistical evaluation. It is highly probably that flaws in testing are large (the fact that numbers on test had a significant effect upon results is indicative of this), but either way the data would imply that selecting the best SchH I animals on the basis of current test results would not necessarily lead to progress in these traits. Pfleiderer-Hogner (1979) suggests the use of a performance test combined with sib selection, but the heritability values do not justify this. In addition, progeny testing, though time consuming, would be a necessary follow-up. A selection index based on tracking and man-work was also suggested, although more success might come from re-evaluating the testing procedure to more accurately reflect genetic aspects.

Temperament

Although most pedigree breeding stems from dogs exhibited in the show-ring the majority of dogs end up living as pets and this is true regardless of breed. The average owner requires an animal that is not nervous or aggressive but has a fairly easy-going and stable temperament. Clearly the character of a dog will be influenced by environmental features, in particular socialization (see Scott & Fuller, 1965; Serpell & Jagoe, Chapter 6). The nature of temperament, in its overall sense, is difficult to define and studies on its heritability are not readily available. Working with 575 US army GSDs, from 18 sires out of 71 dams, Mackenzie, Oltenacu & Leighton (1985) obtained a heritability of temperament of 0.51. Vague as this trait is, the figure is relatively high and suggests that selection for this feature would be successful. Most practical breeders would agree with this viewpoint, which is also in agreement with the Australian guide dog work.

Nervousness

Nervousness is a serious failing in most working dogs outside of sheep herding, and Thorne (1944) put forward the suggestion that extreme shyness is a dominant trait. His study was based on 178 dogs of which 83 were extremely shy. Forty-three of these animals descended from a single basset hound female of extremely shy nature, and he concluded from this that a dominant gene was at work (in contrast to the Fortunate Fields work suggesting a recessive trait). Certainly, Thorne's data were indicative of dominant inheritance, but this is unlikely to be true of all forms of shyness and may only apply to the specific situation he encountered. In their extensive work with pointers, Brown, Murphree & Newton (1978) developed a strain that was normal and friendly towards humans, and a second strain which exhibited extreme human-aversion. In the latter, it was concluded that much of the variability was additive. Character problems in German pointers in respect of gunshyness were reported by Kock (1984), but the heritability derived was only 0.06 ± 0.04 and not significant. Simple explanations for shyness/nervousness are unlikely to be valid and the feature is likely to be both complex in its mode of inheritance as well as in the environmental features which influence it.

In seeking to assess fearfulness in potential guide dogs, Goddard & Beilharz (1985) found Labradors to be less fearful than GSDs that were also more fearful than kelpies and boxers. It is generally held that sheep-herding breeds are more inclined to fearfulness and, despite its present role, the GSD was and still is to some degree a herding breed. Goddard & Beilharz (1985) found considerable within breed variation for fearfulness but no hybrid vigour due to cross-breeding, suggesting a largely additive trait, and this agrees with their high heritability figures (Table 4.1). This implies that within breed selection could be effective and they suggested this for their Labradors. However, they also suggested that selection against fearfulness was likely to be more effective in adults than in pups (Goddard & Beilharz, 1984, 1986).

That closed breeding programmes *can* succeed in enhancing behavioural traits is seen with the British Guide Dogs for the Blind Association where success rates over the past 30 years or so have risen from under 50 to over 90% (D. Freeman, 1988, personal communication). In the USA, Pfaffenberger (1963) described success rates in GSD guide dogs that rose from 9–90% in the 12 years from 1946. Similar closed programs seem desirable for police dogs rather than the current reliance upon 'gift' animals or those bred in 'show' kennels, since such animals may not have been selected for working features. Unfortunately, few British police forces, outside of the Metropolitan, actually have breeding programmes.

The present author has been judging GSDs in the show-ring since the 1950s. During the 1950–60s period it was normal to find up to 20% of animals nervous or fearful. Currently, one would expect to see nervousness only very rarely and 2% would be an approximate value. At first sight this appears to contradict the findings of Mugford & Gupta (1983), who, at Crufts dog show 1982, exposed 203 dogs from 15 breeds to a 60 second stare after which the dog was approached. They found marked levels of nervousness in GSDs. However, the GSD breed in Britain is split into two groups on physical type; one group is based largely on German bloodlines, and the other on 1950/60s British lines. It was the latter that were represented at the Crufts in question. In GSD breeding circles, it is believed that much of the improvement in the character of the breed stems from the use of German imports, all or most of which have been Schutzhund tested, and which tend to exhibit better temperament than the descendants of the 1950s British lines. Testing the British or even American lines would be more likely to reveal temperamental faults than would be the case in German-based bloodlines. Most studies critical of the GSD have been British or American based, rather than European. Researchers are thus assessing specific strains, between which large behavioural differences may exist.

Aggression

In respect of aggression, it is well established that males pose more problems than females (e.g. Beaver, 1983, Borchelt, 1983; Mugford, Chapter 10). Breed differences are claimed. The 'rage' syndrome of the red cocker spaniel is well known, though not actually confined to reds. There seems little doubt that this trait has a genetic basis, although the colour effect may reflect different bloodlines rather than any significance of colour itself. Cocker spaniel breeders do not mate parti-colours to self-colours so that the bloodlines of the two colour phases tend to be distinct. Behavioural differences would tend to reflect this. In foxes, links between certain coat colours and extreme or abnormal behaviour have been identified by Keeler *et al.* (1970) and Belyaev, Ruvinsky & Trut (1981). It seems unlikely, however, that any direct genetic relationships will be found between coat colour and temperament failings in the domestic dog.

Although never followed up, the sudden outbreak of unprovoked aggression among Bernese mountain dogs in Holland (Van der Velden *et al.*, 1976) provided evidence of polygenic inheritance of this trait (Willis, 1989). Lines of Swiss origin, noted for their aggressiveness exist in this breed. Similarly, several studies from the USA report high levels of protective or territorial aggression and fear-biting in GSDs (Beaver, 1983; Borchelt, 1983), though the finding is complicated by the numerical strength of this breed.

The degree to which aggression is acquired or inherited is both controversial and unclear. In the GSD, Wilsson (1985) has shown that social interactions between mothers and offspring during weaning have significant effects upon subsequent pup behaviour. Much trouble with aggression appears to stem from a failure to place *alpha* dogs[3] in the right hands. Most inexperienced owners do not know how to handle such animals, although, in this author's opinion, they often make the best companions as long as one is careful to establish one's authority early on in the relationship. Much of the recent media-alleged problems with Rottweilers may stem from the fact that this breed contains more than its share of *alpha* dogs. On the other hand, the results (unpublished) of this author's recent tests on Rottweilers revealed relatively few *alpha*-type dogs, but a great many owners who did not understand their animals and, in some cases, could not even play with them. Similarly, recent (unpublished) character evaluation studies of Bernese mountain dogs revealed only one *alpha*-type animal. About half the population examined were classified as easy-going and stable, and the rest were equally divided between the categories 'hesitant' and 'nervous/insecure'.

There is a clear difference between the dominant or assertive *alpha* dog and a fighting dog, such as the pit bull terrier. These animals have been deliberately selected for an ability and eagerness to fight, and to this degree are unlike most other breeds of dog in which, as with the wolf, intraspecific aggression tends to be ritualized more often than serious. It is possible that the behaviour patterns of pit bull terriers have been altered by selection to a degree that is not seen in other breeds, even those in which assertive animals are relatively common. Such alteration of behaviour would be a direct result of selection for fighting prowess. That this selection has been so successful in its objective implies that selection in the reverse direction could be equally successful, and that within a few generations pit bull terriers could be changed back into acceptable members of canine and human society.

It may also be important to distinguish between aggression directed against humans and aggression against other dogs. The best bloodlines for working ability in the GSD breed (Perry, 1980) stem from and are still dominated by Vello zd Sieben Faulen (born in 1956) and two important sons, Bernd and Bodo von Lierberg (born in 1962) from whose lines some inter-dog aggression has been apparent. Unfortunately, the most frequently seen bloodlines in the world outside of America now stem from Canto vd Wienerau (1968–72), who was recorded as not being ideal in character and from whom this flaw has doubtless been transmitted, although scientific documentation is not available (see Willis, 1991).

The future of dog breeding

Rightly or wrongly it is a fact that dog breeding in most countries is dominated by the show-ring, which makes it essential that judges in whatever breed discard nervous or aggressive animals, regardless of physical beauty. Hopefully, breeders will then follow this example since winning animals are the ones most

[3] I use the term *alpha* dog in this context to refer to a particular type of animal characterized by: (a) assertiveness in dominance contexts; (b) confidence and lack of nervousness when faced with novel and/or alarming situations or people; and (c) a tendency to protect its owner and owner's possessions. More often than not, these animals are males.

frequently used for breeding purposes. From this perspective, the sooner compulsory character assessments or working tests are introduced the better.

Although sheep-herding has not been discussed here, it is interesting to note that the Border collie has, in the past two decades, moved from the control of the International Sheepdog Society (ISDS) to the Kennel Club (KC), though the ISDS still controls working animals. Although it was decided that a working test would remain for KC registered dogs before they could become full champions, the sad truth is that few Border collies have taken this test and still fewer have passed it. With such failure to attend to essential features, it will be only a matter of time before the ill-named *Show* Border collie will have lost its ability to work. There, if not watched over by the breed societies, will go most working breeds, and this is more likely to happen in Britain and the United States than in continental Europe where breed clubs still control breeding procedures.

There is a need to further document the genetics of canine behaviour. Dogs are usually bred by people who have no training in either behaviour or genetics, despite having a wealth of hands-on practical experience. If canine behaviour is to be modified appropriately, then breeders will need to be able to understand the consequences of their actions, both in terms of breeding as well as husbandry and training. They will need to be able to make sense of new behavioural evidence and, increasingly, they will want to know the extent to which behaviour can be predicted early in life and, if so, how early and by what means.

From a scientific standpoint, dog breeding is likely to change markedly over the next decade, as Best Linear Unbiased Prediction (BLUP)[4] techniques are applied to the process, as they are already to the breeding of farm animals. BLUP techniques, which involve deriving a single breeding value prediction from a number of different information sources, are currently being used to predict such traits as hip dysplasia in dogs (Lingaas & Klemetsdal, 1990; R. Beuing, personal communication). In the future it would be feasible to see BLUP values derived for behaviour traits, although the problem of finding accurate and reliable scoring methods still remains.

Breeders usually select for physical as well as mental traits and, as Mackenzie *et al.* (1986) point out, the genetic relationships, if any, between physical and mental traits need to be documented. There is also a need to determine the degree to which the effects of learning can modify behaviour, and to document and define more accurately the influence of maternal effects.

[4] BLUP techniques take account of information on the dog itself, its parents, siblings, half-siblings and progeny, as well as similar data on the parents and the mates to which the dog was bred. The technique generates a single value – where 100 represents an 'average' animal and values of less than 100 represent superior breeding values and over 100 inferior values – which makes the use of BLUP values easy to apply even if the mathematics of their calculation is complex.

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