Genetics of Behaviour 13

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Introduction

The dog was the first species to be domesticated by man some 10,000 years ago though an association with humans may go back 40,000 years (Clutton-Brock, 1984). Although there has been debate as to the origins of the domestic dog the review by Clutton-Brock (1995) suggests that the wolf is the principal, if not sole, progenitor of the dog. Mitochondrial DNA control region

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sequences of wolves and 67 breeds of dogs suggest that dogs and wolves diverged over 100,000 years ago and that there were four separate occasions when animals which became dogs became distinct from wolves (Vilà *et al.*, 1997, 1999). For this reason dogs are more genetically distinct from one another than if there had been just one instance of separation. From these origins the dog has been diversified into numerous breeds and innumerable shapes. Some of these breeds originated some 3000–4000 years ago (Harcourt, 1974), but others trace back to the Middle Ages and some modern breeds trace, in their present form, only to the end of the 19th century. Because of the wolf relationship considerable attention has been given to the similarities and differences between wolves and domestic dogs but it is inevitable that, after 10,000 years of domestication and living in close proximity to humans, major differences will have evolved. The dog, like the wolf, still rests for 12 hours of every 24, but the human has to some degree determined when and where the dog will rest.

Wolf Behaviour

Although wolves are ancestral to dogs, there are many differences between their behaviour and that of domestic dogs. Some of these differences are due to the fact that domestic dogs are provisioned and usually restrained, so that dogs do not spend long hours hunting or travelling in search of food sources. Wolves dig dens, but dogs rarely do. Vocal communications have also changed; wolves howl more than most breeds of dogs, but they seldom bark. Barking has been selected for in dogs.

Wolves are better at problem solving than dogs. For example, Frank and Frank (1985) found that wolves could learn to manipulate bowls from a box much more quickly than Malamutes, but were worse at passive inhibition (stay training) or active inhibition (leash training) when compared with Malamutes (Frank and Frank, 1982). Furthermore, wolves are very difficult to house-break and are often very destructive. Wolves kept as pets can be very dangerous.

Wolves breed only once a year, and in most cases only the dominant female has a litter (Asa *et al.,* 1985). Most dogs breed twice a year; the Basenji being an exception. Male wolves help to provision the pups. Wolves live in stable packs of up to 15 animals with a dominant pair, but feral dogs live in unstable groups. Wolves travel 120 km per day around territories that vary with the pack size from 40 to 200 hectares (Mech, 1966).

When wolves fight with pack members, they inhibit their aggression if the victim gives submissive and fearful signals such as rolling over, exposing the groin area, avoiding eye contact, tucking the tail, etc. If wolves fight with another pack, the victim will be bitten whether or not he shows submissive signs (Schenkel, 1947).

The effect of human selection on canid behaviour is well exemplified by the study of Goodwin *et al.* (1997). They identified 15 signals in wolves during social interactions and then observed social interactions among dogs

interacting in same-breed groups. Some breeds used very few signals. These authors then plotted the number of signals against physical similarity to wolves. Some breeds such as the French Bulldog and Cavalier King Charles Spaniel neither looked nor behaved like wolves, whereas Alaskan Malamutes looked and acted like wolves. Golden Retrievers behaved more like wolves than their appearance would indicate, but German Shepherd dogs (GSD) behaved less like wolves.

The signals that appear earliest in lupine development are the only ones retained by the non-wolf-like breeds, such as the Cavalier King Charles Spaniel, the Norfolk Terrier, Shetland Sheepdog and French Bulldog (Goodwin *et al.*, 1997).

Major Changes in Behaviour During Domestication

A long-term study (> 40 generations) at the Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirisk, revealed that foxes selected for tameness not only became docile and friendlier towards people, but they also developed curly tails, pendant ears and white spotting (Belyaev, 1979; Trut, 1999; Chapter 2). Piebald spotting is due to the *star* gene and is incompletely penetrant (Belyaev *et al.*, 1981).

On the one hand, the appearance of mutants such as curly tails and pendant ears may not be due to selection for tameness but just coincidental findings in a population undergoing inbreeding due to small effective population size. On the other hand, deliberate selection for tameness in foxes also led to white spotting and selection for spotting in Cocker Spaniels led to less aggression in these Cocker Spaniels (Podberscek and Serpell, 1996) and this is associated with less aggressive breeds such as the Cavalier King Charles Spaniel and Beagle.

Coppinger and Schneider (1995) have ranked breeds of dogs according to their degree of neotenization. Heelers such as Corgis and Huskies are the closest to the adult wild canids. Next, are the headers and stalkers such as the Collie, then the object players such as the hounds, retrievers and poodles (all dependent-eared dogs) and finally those breeds which act adolescent as adults, the Saint Bernard, Komondor, Maremma and Great Pyrenees. Domestication of the dog is not simply a process of neotenization, but breeds selected for certain purposes such as lap dogs (Chihuahua, Pomeranian, Cavalier King Charles Spaniel, French Bulldog) appear and act puppy-like, whereas working dogs and terriers are much less neotenized in appearance and behaviour.

As with other domestic species, there is a relative shortage of scientific data on canine behaviour. Faure (1994) gave some reasons for this which are as valid for the dog as they are for the farm livestock. Faure was referring to in his paper: (i) behaviour is difficult to measure and behavioural traits are often of long duration, making enough data difficult to obtain; (ii) measures of behavioural traits are often not normally distributed, making genetic parameters difficult to estimate; and (iii) the importance of environmental

influences was often overestimated in the past. It can be added that the dog lives in closer communication with humans and is subject to many more varied environmental influences than farm livestock in addition to living in a variety of 'pack' sizes ranging from one upwards. Housing conditions can also influence behaviour (Hetts *et al.*, 1992) as can the interactions between mother and offspring around weaning time (Wilsson, 1984/1985).

According to Mackenzie *et al.* (1986), behavioural work on the dog began around the start of the 20th century, but much of the work was directed towards Mendelian type explanations. Thus, Humphrey and Warner (1934) suggested that gunshyness in the GSD was controlled by a simple gene series with two alleles while Thorne (1944) attributed extreme nervousness in a crossbred population to a single dominant allele.

The Ontogeny of Behaviour and Neotenization

In essence, canine development can be divided into four stages or sensitive periods: the neonatal period, the transition period, the socialization period and the juvenile period. Because some long-term influences on behavioural development may occur *in utero* (Joffe, 1969) an additional prenatal period may be included. The subject has been reviewed by Serpell and Jagoe (1995) who conclude that prenatal effects are unlikely in the dog. In the neonatal period (0–14 days), puppies are in a fairly altricial state; they cannot see, hear or bear weight on their limbs. They can locomote by pulling themselves forward with their forelimbs. They find the mammary gland by tactile cues – warmth, hairlessness and resiliency, and then find the nipple as a protuberance. The neonatal period extends until the puppies open their eyes around day 10. They can learn simple associations, but they are unlikely to be of a lasting nature (Scott and Nagy, 1980). It is, however, thought that daily handling can have long-term effects upon subsequent behaviour (Fox, 1978) and it is known that wolf cubs handled from birth or 6 days were more reliable and friendly than those handled from 15 days or later (Fox, 1971; Zimen, 1987).

The transition period starts from around 2 weeks of age, by which time the eyes are open, and ends about a week later with the opening of the ear canals. The pup's sensory world is now more complete. In this period puppies begin to urinate and defecate without maternal stimulus and they crawl, commence play fighting with siblings and start an interest in solid food. This period corresponds to the wolf cub leaving its nest but, according to comparative studies (Frank and Frank, 1982, 1985; Zimen, 1987), wolves start the transition period slightly ahead of puppies and complete it sooner. According to Scott and Fuller (1965), learning ability in the pup does not reach adult levels prior to an age of 4–5 weeks.

The socialization period was identified by Freedman and his colleagues (Freedman *et al.*, 1961) who found that if a bitch and her litter were completely isolated behind a solid fence for 14 weeks, the puppies were essentially feral and were frightened of people. The socialization period runs through from 3–4

weeks to 14 weeks of age but does not appear to end suddenly with the upper boundary being far from clear-cut. These periods were originally termed critical periods, but now are known as sensitive periods because dogs can be socialized before or after 4–14 weeks, albeit with greater difficulty.

Few puppies have absolutely no socialization. Even the puppy born in a kennel still encounters a human because the bitch is fed and the kennel cleaned. Nevertheless, it is important to expose puppies to people during the second and third months of their lives. Ideally, the people should be those with whom the puppy will spend the rest of its life. For example, a puppy that has not seen a child will not make the ideal pet for a family with small children. Socialization is not only to people, but also to conspecifics. During this period, play among puppies commences and allows puppies to practise adult behaviours and learn which behaviours are acceptable to other dogs.

Work with the Seeing Eye (Guide Dogs for the Blind) by Pfaffenberger *et al.* (1976) led to practical recommendations that socialization between owner and pup should be achieved between 6 and 8 weeks of age. They also suggested that puppies should face their adult conditions of housing at this time. However, Slabbert and Rasa (1993), following work with GSD puppies, came to the conclusion that puppies were best left with their mothers for 12 weeks. This is contrary to the normal rehousing conditions faced by most puppies and does not appear to have been adopted on any real scale by breeders.

The juvenile period follows the socialization period. Puppies may be more fearful and neophobic following the socialization period. Although dogs are believed to reach social maturity between 18 months and 2 years, puberty, which usually occurs between 6 and 9 months, marks the end of the juvenile period because the dog is physically mature. See Fig. 13.1 for more details on development in dogs.

Coat Colour and Behaviour

The relationship of coat colour to behaviour is intriguing. The wild type coat colour for many mammals is agouti – bands of brown (eumelanin) and yellow pigment (phaeomelanin). The precursor molecule for both melanin and the neurotransmitter dopamine is DOPA so that an increase or decrease in synthesis of one will affect the other. When the responses to stress of agouti and non-agouti mice are compared, the non-agouti mice are slower to recover and to reproduce (Hayssen, 1998). Experiments on yellow deer mice indicated that they were tamer and less aggressive than agouti deer mice (Hayssen, 1997).

Hemmer (1990) has shown that coat colour in domestic livestock can be associated with temperament but coat colour *per se* may not be the explanation in this case. Non-white sheep are more likely to lamb out of season than white ones (Dyrmundsson and Adalsteinsson, 1980).

In order to determine whether coat colour was related to aggressive behaviour, the incidence of each coat colour – black, yellow and chocolate – among all the Labrador Retrievers that were patients at The Veterinary Medical

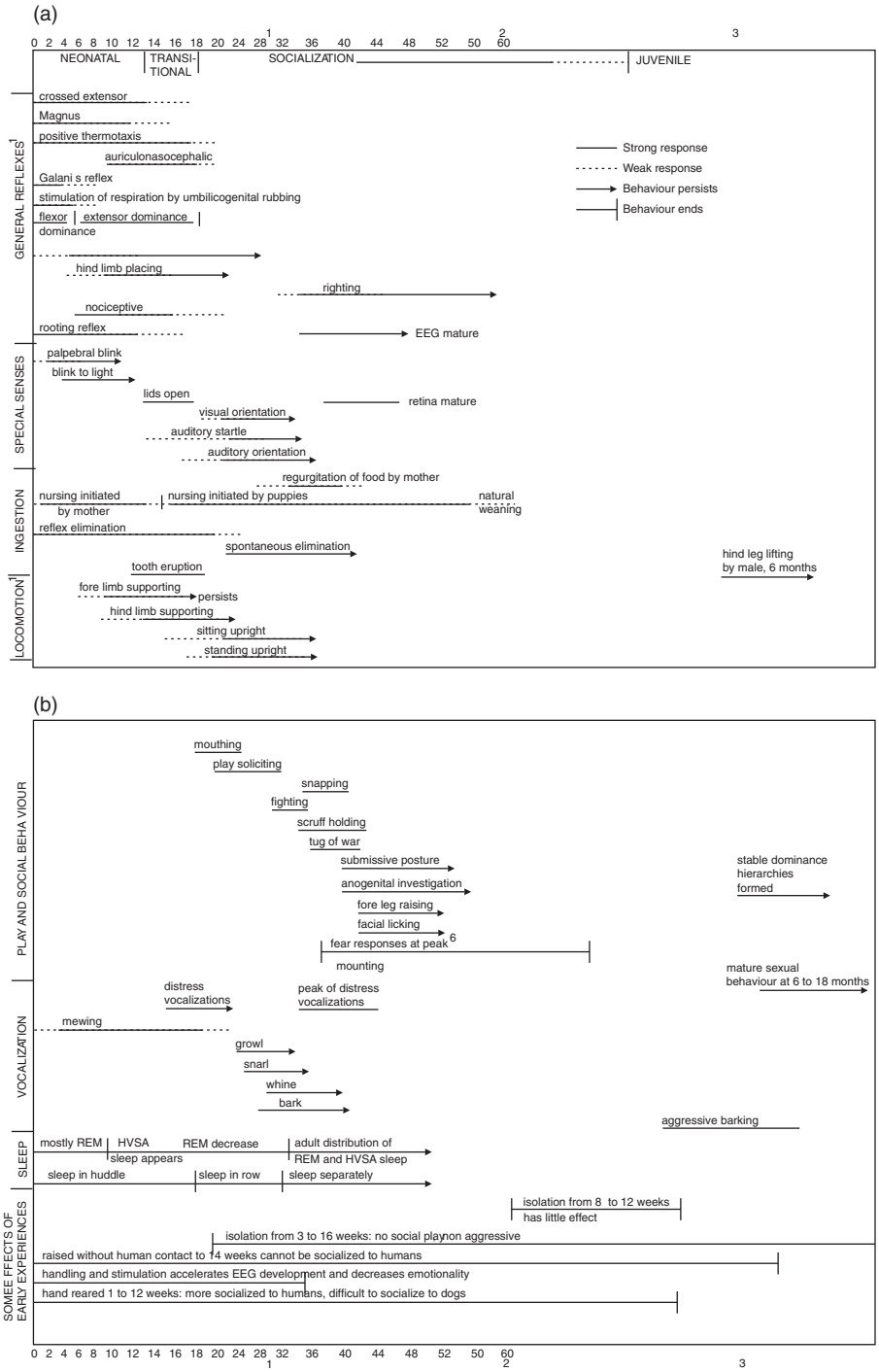

Fig. 13.1. The development of the dog (Houpt, 1998; with permission from Iowa State University Press).

Teaching Hospital of Cornell University was compared to the incidence of the three coat colours among Labradors presented to the Animal Behavior Clinic for aggression. Chocolate Labradors were less likely to be presented for behaviour problems than their numbers in the hospital population would have predicted. Black Labradors (the dominant colour in this breed) were presented for aggression in proportion to their numbers whereas yellow Labradors tended to be over-represented for aggression (Fig. 13.2).

The effect of breeding foxes for tameness has revealed that piebald foxes are tamer than their solid colour counterparts (Trut, 1999). Podberscek and Serpell (1996) found that solid colour Cocker Spaniels were more likely to be aggressive than white spotted ones (particolours). Between the solid colours, red Cocker Spaniels were more likely to be aggressive than black ones. It is known that bloodlines of reds, blacks and particolours tend to be distinct (Lloyd Carey, 1992) and what may be being observed is an inherited trait that arose in some red line and has remained predominant in reds because of largely separate breeding policies.

Genetics and Behavioural Selection of Working Dogs

Dogs have not only developed over a large range of body sizes with, for example, a Chihuahua being a tiny portion of the body weight of a St Bernard,

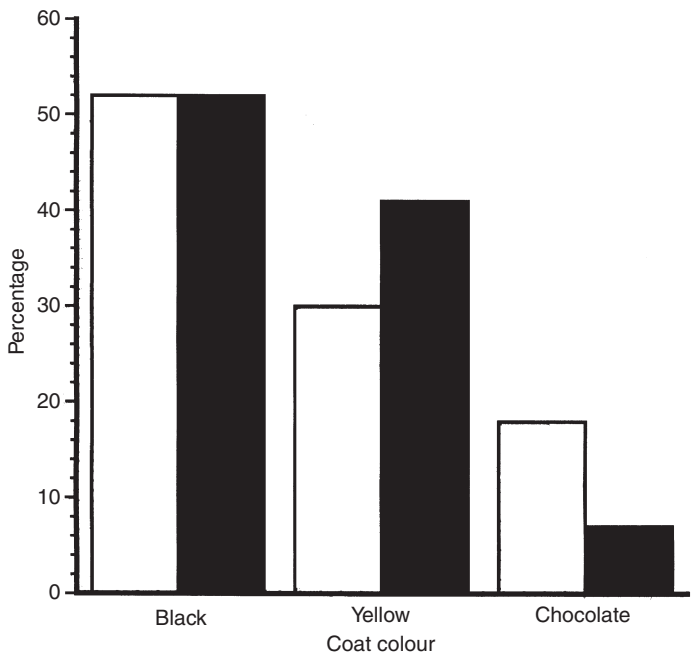

Fig. 13.2. A comparison of the proportion of Labrador Retrievers presented for medical problems (□) with those presented for aggression (■).

but they have also developed to undertake a variety of different purposes. Without herding breeds such as the Border Collie or the Kelpie, the handling of European, Australasian and American sheep on a large scale would be well nigh impossible. Similarly the non-deployment of livestock protection dogs such as the Maremma, Great Pyrenees or Anatolian Shepherd dog would make sheep losses to predators unacceptable in parts of North America. In addition to these tasks, dogs serve as drug/explosive detection animals, as general purpose police dogs, as gundogs, sled dogs, trackers and hunting dogs, as eyes for those who cannot see and ears for the deaf, as well as just companions to those whose lives might be less full without them.

This plethora of activities for which dogs are employed may be taken to mean that humans have selected for these features over a period of time. It would however be erroneous to suggest that humans have been selecting for a specific feature over many millennia. As Coppinger and Schneider (1995) have suggested, most traits may be a fortuitous accident. Many of the distinguishing features of some dog breeds such as hanging ears, curly tails, long coats, hanging jowls and various coat colours have no real selectional advantage (Bemis, 1984). They may have arisen by chance and been retained for their distinguishing nature or by the desire to retain the dog in a juvenile state (Frank and Frank, 1982).

Guide dogs for the blind

Guide dogs are a product of the early 20th century, primarily using GSD and more recently greater use of Labrador and Golden Retrievers and their crosses. Initially, dogs were selected from gift dogs with a high failure rate (Scott and Bielfelt, 1976; Goddard and Beilharz, 1982) but more recently guide dog organizations have undertaken their own breeding programmes with greater success. American studies (Bartlett, 1976; Scott and Bielfelt, 1976) tended to show low heritabilities for most traits even though based, in Bartlett's case, on over 1800 animals. In most instances heritabilities did not differ significantly from zero. The later Australian work based on 394 Labrador Retrievers (Goddard and Beilharz, 1982) also showed low values but not for fear, the major cause of guide-dog failure, or for overall success (Table 13.1). Both these had moderate heritabilities which, although specific both to the population under study and the time that the work was undertaken, could explain why guide dog breeding kennels now have higher rates of success.

In addition to moderate heritabilities for fear or 'nervousness' strong positive correlations were observed with 'sound shyness' and negative correlations with 'willingness' (see Table 13.2). Most breeders believe that nervous animals give rise to nervous animals in increased proportions and, though empirical, this would seem to be borne out by the Australian work (see Goddard and Beilharz, 1983, 1984, 1985, 1986). It also substantiates the work on Pointers selected for fearfulness (Brown *et al.*, 1978). In many breeds, breeding programmes are dictated by the show ring. Thus conformational features rank

Table 13.1. Heritability estimates for guide dog traits

	Sire		Dam		Combined	
Trait	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	0.09	0.17	0.13	0.09	0.08

Goddard and Beilharz (1982).

Table 13.2. Genetic correlations (below diagonal) and heritabilities (diagonal) in Labrador Retrievers

Trait	N	S	C	W	D	SS	BS
Nervousness (N)	**0.58**						
Suspicion (S)	0.53	**0.1**					
Concentration (C)	–0.01	–0.31	**0.28**				
Willingness (W)	–0.57	–0.2	0.67	**0.22**			
Dog distraction (D)	0.11	0.63	–0.5	–0.41	**0.08**		
Sound-shy (SS)	0.89	0.47	0.33	–0.78	0.28	**0.14**	
Body sensitivity (BS)	0.72	0.51	–0.3	–0.74	–0.21	0.59	**0.33**

Goddard and Beilharz (1983).

high, yet the majority of puppies end up in pet homes far removed from the show ring. Attention to behavioural traits and character are crucial in breeding puppies going to the pet market. According to Mugford and Gupta (1983) undesirable character traits seen on the bench were not apparent in the confines of the show ring. This work seems to fail to appreciate that a dog may be protective on a bench yet not in the ring. Nevertheless it is true that many judges fail to recognize or appreciate character failings and the sort of dog being exhibited could reflect the judges' discriminatory ability. Some effective character test for show dogs would thus seem desirable.

Hunting dogs

Although hunting was believed to be a major use of the dog in its first associations with humans (Clutton-Brock, 1995) there are those who question this (Manwell and Baker, 1984). Nevertheless men have used dogs for hunting at least from some 3000 years BC (sight hounds) and in more recent centuries as pack animals pursuing fox or deer and as gundogs in a variety of roles. A German study on German Wire-haired Pointers (Geiger, 1972) looked at four major traits and found that, although maternal heritabilities were high, sire values did not differ from zero (Table 13.3). More recently Scandinavian workers have sought to examine the genetics of hunting traits in English

Setters and Finnish Spitz (Vangen and Klemetsdal, 1988). The studies were based on 5285 English Setter tests and 4864 Finnish Spitz tests. Heritability studies were higher in English Setters than Finnish Spitz but none were substantial (see Tables 13.4 and 13.5). It was pointed out that some traits did not show a normal distribution but breeding values were calculated from some of the Finnish Spitz traits. It was concluded by the researchers that the 'scoring' of hunting traits was probably the reason for low heritabilities and that better scoring techniques could lead to greater progress in hunting dogs.

Schmutz and Schmutz (1998) calculated heritabilities on seven hunting traits in five breeds using tests devised by the North American Versatile Hunting Dog Association (NAVHDA). Values are shown in Table 13.6 and

Table 13.3. Heritability estimates in German Wire-haired Pointers

Trait	Sire	Dam
Hare tracking	0.03	0.46
Nose	0.01	0.39
Obedience	0.01	0.19
Seek	0	0.41

Geiger (1972).

Table 13.4. Genetic (above diagonal) and phenotypic (below diagonal) correlations and 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)	0.8	0.74	0.64	0.61	**0.17**

Vangen and Klemetsdal (1988).

Table 13.5. Genetic (above diagonal) and phenotypic (below diagonal) correlations and heritabilities (diagonal) for Finnish Spitz

Trait	TS	SA	FB	MK	BK	HB	FB	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**	0.22	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 (FB)	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**

Vangen and Klemetsdal (1988).

Table 13.6. Heritabilities of hunting traits using the NAVHDA test and midparent–offspring regression

	German SH Pointer		German WH Pointer		Griffon		Large Munsterlander		Poodle Pointer		Overall	
Trait tested	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE
Number of dogs	80		99		75		86		144			
Nose use	0.35	0.11*	0.32	0.12	0.33	0.08*	0.19	0.12	0.19	0.07*	0.02	0.04
Search	0.48	0.07*	0.31	0.10*	0.18	0.12	0.19	0.11	0.12	0.08	0.19	0.05*
Water retrieve	0.13	0.01	0.32	0.28*	0.30	0.10	0.24	0.16	0.31	0.09*	0.17	0.07*
Pointing	0.25	0.22	0.13	0.22	0.13	0.09	0.31	0.11*	0.10	0.15	0.18	0.08*
Tracking	0.48	0.09*	0.14	0.12	0.13	0.08	0.80	0.10	0.17	0.06	0.07	0.06
Desire to work	0.31	0.12*	0.14	0.10	0.2	0.10	0.22	0.11	0.05	0.08	0.10	0.05
Cooperation	0.22	0.12	0.34	0.11*	0.08	0.09	0.25	0.11	0.09	0.07	0.13	0.04*
Weighted total score	0.34	0.13*	0.27	0.14	0.22	0.10	0.33	0.13*	0.08	0.08	0.09	1.13

*$P < 0.05$.
After Schmutz and Schmutz (1998).

were significant only in those marked with an asterisk. The authors suggested that low values may indicate an advanced state of development in these breeds and thus reduced variation. Repeatabilities of NAVHDA tests were low and non-significant but dogs taking second tests were those which had failed originally and thus could have undergone extra training to seek to improve.

Police and armed service work

Dogs were used in the First World War (1914–1918) by most participants, with the British relying on Airedales and the Germans on GSD. Since that time the GSD has been the principal breed used by police and armed forces around the world. In more recent times gundogs such as English Springer Spaniels, Cocker Spaniels and Labrador Retrievers have been used in drug and explosive detection work, not through any lack of ability of the GSD but because of its tendency, when seeking drugs, to have part of its attention on the protection role, which gundogs do not have.

Heritability studies on Swedish army dogs (GSD) were undertaken by Reuterwall and Ryman (1973) based on over 900 animals bred in the training centre at Solleftea, puppy walked in private homes and then temperament tested at 18 months. Heritability estimates were derived from their data by Willis (1976) and are shown in Table 13.7. Values were disappointingly low but, as Mackenzie *et al.* (1986) suggested, the scoring system was complex and 18 month assessments may not be truly reflecting inherited differences. This may be equally true of the study of Schutzhund testing by Pfleiderer-Hogner (1979). Schutzhund testing comes in three grades termed SchH I, SchH II and SchH III with the higher numbers indicating more advanced work. Each test involves tracking, obedience, man work (protection) and character (courage). Thousands of tests are undertaken on GSDs in Germany each year and

Table 13.7. Heritabilities (half sib) of mental traits in German Shepherd dogs

	Paternal half-sib values	
Trait	Males	Females
Number of animals	488	438
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

*$P < 0.05$, **$P < 0.01$.
Willis (1976) after Reuterwall and Ryman (1973).

show dogs must obtain specific SchH grades to be exhibited as adults. Pfleiderer-Hogner analysed 2046 tests on 1291 GSDs from 37 sires with all testees being born in 1973. Her heritability figures did not differ from zero whether derived from sire/dam or combined components. She did, however, obtain a phenotypic correlation between Man Work and Courage of 0.76 ($P < 0.001$). It is difficult to believe that Schutzhund testing has no genetic value and one has to conclude that either the traits are under non-additive control or that, as with hunting dogs, the flaws in testing are serious enough to recommend new designs of testing which, 21 years later, has not happened. The latter explanation is more likely.

Tracking is an important feature for all police and service dogs. Pioneering work by Kalmus (1955) showed that dogs could distinguish between the body odours of different individuals, even of the same family and twins. King *et al.* (1964) found that dogs were beginning to fail to detect human odour after 7–14 days when samples were kept outside but could detect samples kept indoors for up to 6 weeks. Dogs joining a track at some mid-point are expected to go in the forward direction of the track but Mackenzie and Schultz (1987) showed that this was not the case. Even within a tracking breed, dogs vary in their ability for, and interest in, tracking but the genetic basis – if any – is as yet unclear.

An important feature of a working dog would be a good standard of hip conformation or an absence of hip dysplasia. In a study of 575 GSD army dogs, Mackenzie *et al.* (1985) graded hip dysplasia and temperament each on a scale of 1–9 with higher numbers being better. They found a heritability of 0.26 for dysplasia and 0.51 for temperament with a negative genetic correlation of –0.33. This suggests that better hips were associated with poorer temperaments, which is difficult to explain when a positive correlation might have been expected. This does, however, suggest that physical and mental traits may be linked.

Herding dogs

Herding breeds such as the Border Collie and Kelpie herd livestock, usually sheep, from one location to another. That they can do so relies as much upon the sheep being selected to flock combined with their flight behaviour as it does on the dog's instinctive ability to chase and nip. Some breeds like the GSD were used, in addition, to patrol the edge of an unfenced field acting in the role of a mobile fence to keep sheep on one side. Failure to select for sheep working potential means that most modern GSD have no sheep working instinct although a few lines exist based on HGH (a sheep working qualification) animals. Most breeds herd silently with their head down but some breeds like the New Zealand Huntaway work with head erect and are vocal. It has long been assumed that the herding dog is acting in a similar manner to its wolf ancestor stalking prey but, whereas the wolf stalk ends with a kill, the Collie stalk ends in moving or holding the sheep.

As Burns (1969) has pointed out, a Border Collie should understand and respond to at least eight commands to work effectively. Some dogs show 'eye' which means that they lower their head, half crouch and stare fixedly at the sheep. Other dogs may 'clap' that is they drop to the ground and may crawl towards the sheep or may get up and rush at them. Breeders select for such traits, but the mode of inheritance is unclear. Faced with African sheep, an ability to bark and move at the sheep was found to be necessary (Burns, 1969). It is astonishing to realize that the mode of inheritance of sheep work is little understood despite the value of the sheep industry world-wide and the absolute necessity to use dogs to handle sheep effectively. Jasper Rine and his colleagues (McCaig, 1996) are, as described below, attempting to find the genes for these traits in Border Collies and hybrids.

Livestock protection dogs

Livestock protection or guarding dogs trace back many centuries in their use for protecting sheep flocks. Most breeds doing this task today tend to be white in colour, whereas herding breeds are not. Breeds such as the Pyrenean Mountain Dog, Maremma, Komondor and Anatolian Shepherd are the modern-day descendants. Such dogs have no herding instinct but develop instinctive protectionist traits against predators (Linhart *et al.*, 1979; Coppinger *et al.*, 1983, 1985, 1988; Green, 1990). In the USA, the predators would be the coyote, the cougar, dogs and perhaps bears and re-introduced wolves. The role of the guarding dog is not to engage the predator in a fight but to frighten it away by the implied threat of a fight (Black, 1987).

It does appear that the livestock guarding breeds have a basic instinct. Breed differences in effectiveness were not significant for Great Pyrenees, Komondor, Askbash, Anatolians, Maremmas and hybrids (Green and Woodruff, 1983a,b,c, 1987; Green, 1989). All were aggressive towards predators, other dogs and occasionally people. It was seen that dogs reared with livestock by 8 weeks of age were more successful than those placed with livestock at an older age (Green and Woodruff, 1988). It is known that behavioural differences between herding and guarding breeds exist (Coppinger *et al.*, 1987), with the former showing a high level of partial predator behaviour and the latter a high level of agonistic play. According to Coppinger and his colleagues (1987) the two types of livestock dog are neotenic polymorphs unconsciously selected by differential retardation of ontogeny.

Genetics and Behavioural Selection of Pet Dogs

Breed differences

Scott and Fuller (1965) at Jackson Laboratory in Bar Harbor, Maine, performed the most comprehensive study of genetic differences in canine behaviour.

They used five breeds: Cocker Spaniels, Beagles, Shetland Sheepdogs, Basenjis and Wire-haired Fox Terriers. They performed a battery of tests to determine genetic differences in behaviour. Cocker Spaniels were the easiest to teach to sit quietly. The different breeds acted differently in response to leash training. Cocker Spaniels and Beagles were easiest to leash train and Basenjis were the worst; they baulked, fought the leash and strayed out of position. Shetland Sheepdogs fought the leash whereas Beagles were vocal (Fig. 13.3). Basenjis gave the best performance in reward training and Shetland Sheepdogs the worst, but the authors noted that the Shetland Sheepdogs were not as food motivated. Basenjis were best and Shetland Sheepdogs worst on a motor skill test in which the dogs had to climb a ramp and walk along a narrow elevated platform. Later, Scott and Fuller tested problem solving. The dogs had to learn to pass around a barrier to reach a dish of food instead of travelling directly to the dish. The next test involved pulling a dish from under a barricade. There were no particular breed differences in those two tasks. Beagles were best at learning a six choice point maze. A trailing test was administered in which fish was used to entice the dogs to follow a specific route. There were no breed differences. Cocker Spaniels were most successful and Shetland Sheepdogs the

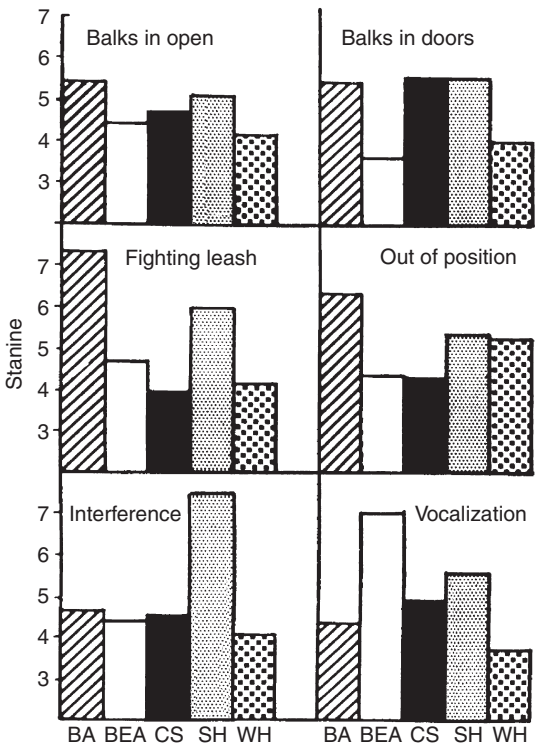

Fig. 13.3. Errors made by five breeds of dogs during leash training: BA = Basenji, BEA = Beagle, CS = Cocker Spaniel, SA = Shetland Sheep Dog, WH = Wire-haired Fox Terrier (with permission from University of Chicago Press).

worst in a problem solving test in which the dogs had to climb a ramp and walk across a narrow plank and to find a food reward. When testing puppies for complete dominance within litters of puppies, Scott and Fuller found that Wire-haired Fox Terriers, Shetland Sheepdogs and Basenjis showed complete dominance by 1 year of age, but Cocker Spaniels and Beagles did not. Dominance was determined by control of a bone.

Hart and Hart (1985) looked at 13 traits thought to be of importance to dog owners and then ranked 56 breeds on the opinions of 48 obedience judges and 48 veterinarians. Each person ranked only seven breeds. The authors then used analyses of variance to determine the magnitude of the *F*-test as a means of distinguishing between breeds. The results are summarized in Table 13.8 and indicate that features such as excitability and excessive barking were reliable means of distinguishing between breeds, whereas the ease with which a breed was house-trained was not. Thus, the Rottweiler ranked in the lowest decile for excitability but the highest for watchdog barking, whereas the Bloodhound ranked in the lowest decile on both traits and the GSD intermediate on excitability and the highest on watchdog barking. Allocating genetic parameters to such traits has not yet been done. Judges and veterinarians could be biased and limited in their knowledge of some breeds but in this instance concentrated on seven breeds each which they were obviously familiar with. The test may have flaws but the results seem feasible to those practically involved with dogs.

Hart and Hart (1985) found that cluster analysis revealed that three factors: reactivity, aggression and trainability, could explain most of the 13 traits. Not all aggression fell into the aggression factor; snapping at children clustered with reactivity. The breeds believed to be most likely to snap at children were:

Table 13.8. Behavioural traits ranked in decreasing order in differentiating between dog breeds

Trait	*F* Ratio
Excitability	9.6
General activity	9.5
Snapping at children	7.2
Excessive barking	6.9
Playfulness	6.7
Obedience training	6.6
Watchdog barking	5.1
Aggression to dogs	5.0
Dominance over owner	4.3
Territorial defence	4.1
Affection demand	3.6
Destructiveness	2.6
House training ease	1.8

Hart (1995).

Scottish Terrier, Miniature Schnauzer, West Highland White Terrier, Chow Chow, Yorkshire Terrier and Pomeranian. In a similar study performed in the UK, Bradshaw *et al.* (1996) ranked dogs according to cluster analysis using factors for aggression, reactivity and immaturity. The latter include traits such as playfulness and destructiveness. Dogs could rank high, average or low for each factor, giving eight categories. Breeds that ranked high in aggression, average reactivity and low immaturity were Rottweilers, GSD, Doberman Pinschers and Bull Terriers. Those which ranked low in aggression, high reactivity and low immaturity were King Charles Spaniels and Shetland Sheepdogs.

Intelligence and trainability

Coren (1994) surveyed 208 obedience judges from the USA and Canada. He concluded that for obedience and working intelligence, the top five breeds were Border Collie, Poodle, GSD, Golden Retriever and Doberman Pinscher (see Table 13.9). Coren admits that to do a scientifically valid test would require 25 people working for 3–5 years and cost US$14,000,000. Coren also performed a series of intelligence tests on many breeds of dogs. The tests he performed on a small number of dogs of each breed involved long- and short-term memory (finding food under one of several cups), problem solving using barriers, response to own or another name, reaction to a rearrangement of the furniture, etc. The highest overall (both memory and problem solving) were Doberman Pinschers, GSDs, Norwegian Elkhounds, Poodles, Pulis and Shetland Sheepdogs. His ranking for adaptive intelligence is shown in Table 13.11. Perhaps the most interesting observation on canine learning is that dogs in a companionship relationship with humans had decreased performance on problem solving compared with those that had a working relationship with humans (Topál *et al.*, 1997).

Table 13.9. Ranking of dogs for obedience and working intelligence

Rank	Breed
1	Border Collie
2	Poodle
3	German Shepherd
4	Golden Retriever
5	Doberman Pinscher
6	Shetland Sheepdog
7	Labrador Retriever
8	Papillon
9	Rottweiler
10	Australian Cattle Dog

Coren (1994).

Aggression

Because the dog lives in close association with humans, its behaviour is of great importance to the well-being of both. Although various behavioural traits are important to owners the main problem with dogs that affects this relationship is aggression towards humans (Mugford, 1995). Sudden unprovoked aggression against owners and their families was observed in Bernese Mountain Dogs in the Netherlands (Van Der Velden *et al.*, 1976). Data on 404 animals were obtained, with aggression being graded into five categories of severity. Willis (1998) has tabulated these data, and it can be seen (Table 13.10) that increasing aggression grade of parents led to a definite increase in grade of aggression of progeny, which is indicative of a polygenic trait.

There are two types of canine aggression, desirable and undesirable, from a human standpoint. Several breeds of dogs have been selected for aggression, particularly aggression to strangers. Rottweilers, Doberman Pinschers, German Shepherds and Akitas are examples of breeds selected for that behaviour,

Table 13.10. Highest ranking dogs for adaptive intelligence

Highest overall intelligence	Good in learning and memory	Good in problem solving
Doberman Pinscher	Beagle	Australian Terrier
German Shepherd dog	Belgian Malinois	Basenji
Norwegian Elkhound	Belgian Sheepdog	Cairn Terrier
Poodle	Belgian Tervuren	Chihuahua
Puli	Bernese Mountain Dog	Fox Terrier
Shetland Sheepdog	Border Collie	Kerry Blue Terrier
	Bouvier des Flandres	Malamute
	Golden Retriever	Samoyed
	Labrador Retriever	Schipperke
	Welsh Corgi	Schnauzer
		Siberian Husky
		West Highland White Terrier

Breeds listed in alphabetical order. From Coren (1994).

Table 13.11. Aggression in Bernese Mountain dogs

Parents (at least one)	Number of progeny	Progeny grades					Mean grade
		1	2	3	4	5	
Grade 1	131	58.8	5.3	28.2	2.3	5.3	1.9
Grade 2	63	41.3	9.5	36.5	6.3	6.3	2.27
Grade 3	136	36.8	4.4	36.8	4.4	17.6	2.62
Grade 4	41	19.5	4.9	51.2	9.8	14.6	2.95
Grade 5	114	25.4	0.9	31.6	6.1	36.0	3.62
Total	485	39.2	4.5	34.4	4.9	16.9	2.56

After Van Der Velden *et al*. (1976).

and Hart and Hart (1985) found that those breeds were in the top decile for territorial defence. Many trainers believe that dogs are aggressive because their owners spoil them. According to Voith *et al.* (1992) dogs whose owners reacted anthropomorphically were no more likely to have behaviour problems.

No matter how desirable a dog is for protection, nobody wants a dog that bites him or her. The Hart and Hart (1985) study indicated that Fox Terriers, Siberian Huskies, Afghans, Miniature Schnauzers, Chow Chows and Scottish Terriers were most likely to be dominant over the owner. Dogs that attack other dogs can also be a problem. Scottish Terriers, Miniature Schnauzers, West Highland White Terriers, Chow Chows and Fox Terriers were believed to be the breeds most prone to this problem. Some breeds have been selected deliberately for fighting purposes, e.g. the American Pit Bull Terriers and increasingly steps are being taken by governments to control the breeding of such dogs. Politicians have to be careful that the right breeds are targeted.

Aggression may not be a unitary phenomenon, but there is considerable disagreement in how to subdivide it. Overall (1997) has 13 subcategories – maternal, play, fear, pain, territorial, protective, interdog, redirected, food-related, possessive, predatory, dominance and idiopathic aggression. Askew (1996) has 11: dominance, possessive, protective, predatory, fear, intermale, interfemale, pain-elicited, punishment-elicited, maternal and redirected aggression. Landsberg *et al.* (1997) listed the types of aggression as dominance, possessive, fear, territorial, predatory, pain, interdog, redirected, maternal and intraspecies, idiopathic and learned. Houpt (1998) has fewer categories: territorial, fear (including fear of pain), predatory, maternal, interdog and owner-directed (dominance).

Borchelt (1983) defined aggression in the dog in eight ways. These were fear-elicited (22), dominance aggression (20), possessiveness (17), protectiveness (17), predation (1), punishment-elicited (7), pain-elicited (2) and intraspecific aggression (12). The figures in brackets refer to the percentage of cases in the examination of 245 cases of aggressive behaviour. Breed differences were reported, with breeds like the Doberman Pinscher, Toy Poodle, Lhasa Apso and English Springer most likely to show dominance aggression. In contrast, working breeds, notably the GSD, showed more protective aggression and fear-elicited aggression was most likely in GSD and commonly seen in Cocker Spaniels (Borchelt, 1983). Similar findings were seen by Beaver (1983, 1993). In a smaller series, Line and Voith (1986) found that mixed breeds, Cocker Spaniels, English Springer Spaniels, Lhasa Apsos, Miniature Poodles and Brittany Spaniels were most likely to be presented for dominance aggression. The pure breeds of dogs most likely to be presented to five referral practices for aggression are shown in Table 13.12. Springer Spaniels, Wheaten Terriers, Doberman Pinschers, Old English Sheepdogs and Dalmatians appeared out of proportion to their breed registration (Landsberg, 1991). Notice that Springer Spaniels are included in the list from several clinic studies despite the fact that this is not a numerous breed in America.

It is difficult to decide which populations to use as a control for the behaviour cases. The national kennel club registration numbers, which

Landsberg (1991) used, or the dogs presented for behaviour problems can be compared with dogs presented for medical problems, but the breeds may vary in number geographically. Table 13.13 compares kennel club registration with breed incidence of aggression. The hospital population is more likely to reflect the breeds in the surrounding area, but, depending on the specialist in a referral hospital, some breeds may be over-represented. For example, dogs with progressive retinal atrophy are more likely to be presented if there are board-certified ophthalmologists on the staff.

Table 13.12. Breeds of dogs most frequently presented because of aggression

New York City[a]	Texas[b]	Toronto[c]	Kansas City[c]	Ithaca, NY[c]
German Shepherd	Cocker Spaniel	Cocker Spaniel	Cocker Spaniel	Springer Spaniel
Cocker Spaniel	German Shepherd	Springer Spaniel	Poodle	Cocker Spaniel
Poodle (all)	Springer Spaniel	Golden Retriever	Irish Wolfhound	German Shepherd
Lhasa Apso	Schnauzer (all)	Lhasa Apso	Golden Retriever	Golden Retriever
Doberman Pinscher	Dalmatian	Wheaten Terrier	German Shepherd	Lhasa Apso
Springer Spaniel	Basset Hound	Schnauzer	English Bulldog	Doberman Pinscher
	Old English Sheepdog	Bull Terrier	Dachshund	Labrador Retriever
	Poodle (all)	German Shepherd	Chow Chow	Poodle (all)
	Wire-haired Fox Terrier			

[a]Borchelt (1983), [b]Beaver (1983), and [c]Landsberg (1991).

Table 13.13. Breed incidence of behaviour problems in comparison to breed registration

Behaviour problems	CKC Registration 1989	AKC Registration 1989
Springer Spaniel	German Shepherd	Cocker Spaniel
German Shepherd	Labrador Retriever	Labrador Retriever
Cocker Spaniel	Poodle	Poodle
Golden Retriever	Shetland Sheepdog	Golden Retriever
Labrador Retriever	Golden Retriever	German Shepherd
Lhasa Apso	Cocker Spaniel	Rottweiler
Doberman Pinscher	Shih Tzu	Chow Chow
Poodle	Schnauzer	Dachshund
Dachshund	Lhasa Apso	Schnauzer
Schnauzer	Yorkshire Terrier	Beagle
Shetland Sheepdog	Rottweiler	Shetland Sheepdog
Wheaten Terrier	Pomeranian	Yorkshire Terrier
Old English Sheepdog	Siberian Husky	Shih Tzu
Yorkshire Terrier	Bichon Frise	Pomeranian
Beagle		Lhasa Apso
Dalmatian		

CKC = Canadian Kennel Club, AKC = American Kennel Club. All breeds listed in order of frequency.
Landsberg (1991).

In a study from the Animal Behaviour Clinic, College of Veterinary Medicine, Cornell University, the most frequently represented breeds presented for aggression toward strangers and for separation anxiety were compared to the breeds most often presented to the Veterinary Medical Teaching Hospital over the same time period (Takeuchi *et al.*, 2001; Table 13.14). Only individual breeds with ten or more dogs in at least one of the behaviours were evaluated. English Springer Spaniels were significantly more common among dogs with aggression to owners (10.7%) than among those with aggression to strangers (0%) ($P = 0.002$). Among dogs with aggression to strangers, 12% were Labrador Retrievers as compared to none observed among dogs with aggression to owners ($P < 0.0001$). English Springer Spaniels and Rottweilers (but not German Shepherds) had significantly ($P < 0.005$) greater representation among dogs with aggression to owners as compared to the hospital population. This is the first study to reveal that Rottweilers are presented more frequently than expected for dominance aggression. There was a significantly ($P = 0.02$) higher proportion of GSDs (but not Labrador Retrievers) among dogs with aggression to strangers as compared to the proportion observed in the hospital population. Other breeds were not evaluated, in light of the small numbers.

It is interesting that all four studies indicated that English Springer Spaniels are frequently presented for dominance aggression (Borchelt, 1983; Landsberg, 1991; Line and Voith, 1986; Takeuchi *et al.*, 2001). The changes in neurotransmitter levels in English Springer Spaniels indicate that a genetic cause, even a single gene, might be responsible. There does appear to be decreased levels of serotonin and dopamine metabolites in the cerebrospinal fluid of English Springer Spaniels euthanized for aggression (Reisner *et al.*, 1996). A survey of Springer Spaniel owners indicated that over 20% of English Springer Spaniels have bitten people (Reisner, 1996).

When all behaviour problems were combined, Wright and Neselrote (1987) found that sporting breeds were presented more often, followed by mixed breeds, working dogs, terriers, non-sporting, hounds and toys. The specific breeds of dogs most likely to be presented were Cocker Spaniels, GSDs, English Springer Spaniels, Doberman Pinschers, Golden Retrievers and Dachshunds.

Table 13.14. A comparison of breeds presented for behavioural problems with those presented for medical problems

Aggression to owner	Aggression to strangers	Separation anxiety	Hospital
English Springer Spaniel	Labrador Retriever	Labrador Retriever	Labrador Retriever
Rottweiler	German Shepherd	Dalmatian	Golden Retriever
German Shepherd	Dalmatian	Cocker Spaniel	German Shepherd
		Beagle	Cocker Spaniel
			Rottweiler

Takeuchi *et al*. (2001).

Abnormal behaviour

A long term study on Pointers selected for human aversion in comparison with a line selected for normal behaviour has been an interesting study on the genetics of behaviour. The nervous line was hypervigilant with a strong avoidance of humans and a low flight threshold. The nervous Pointers were much slower to learn operant conditioning (pressing a lever for a food reward), but were better at classical conditioning (pairing a sound with shock). They froze at loud sounds and would not approach a person (Dykman *et al.*, 1969). Phenothiazine-derivative tranquillizers were not effective in overcoming the fearful responses (Angel *et al.*, 1974). The nervous line showed a high sensitivity to the mange mite but few biochemical differences (DeLuca *et al.*, 1974). Inbreeding levels reached values in excess of 40% in the timid strain but inbreeding had minimal effect and it was concluded that human aversion was largely caused by additive genetic effects, suggesting a high heritability (Brown *et al.*, 1978).

Obsessive compulsive behaviour

Among the most interesting behavioural abnormalities are stereotypic or compulsive behaviours (Luescher, 1998). These are repetitive non-functional behaviours. They include circling, which is seen in Bull Terriers (Dodman *et al.*, 1996) and in a slightly different presentation in German Shepherds (Hewson *et al.*, 1998), digging as if for vermin by Rottweilers, anal checking by Schnauzers and flank sucking by Doberman Pinschers. The breed predispositions indicate a hereditary basis.

Sex differences in behaviour

The reaction of dogs to humans is very much influenced by the sex of both the dog and the human. Lore and Eisenberg (1986) found that in a kennel situation female dogs showed little reluctance to approach humans of either gender but male dogs were much less likely to make body contact with unfamiliar men. Wells and Hepper (1999) showed that the gender of both human and dog had an effect upon response that the dog displayed in some traits such as barking and eye orientation. This could have a bearing upon kennel staff, with females being more widely acceptable than males as regards relationship with the dog.

Hart and Hart (1985) found that obedience judges and veterinarians felt that male and female dogs differed in ten of 13 traits. Females were easier to house-break and obedience train. Females demanded more affection. Males were more playful and active, but were more likely to be aggressive to other dogs, to snap at children and to be dominant over the owner. Male dogs were also more likely to exhibit territorial defence.

According to Borchelt (1983), males were more aggressive than females and entire males more so than neutered males, while the reverse situation applied in females. Males were more likely to be presented for dominance and territorial aggression (Landsberg, 1991). Wright and Neselrote (1987) found that males outnumbered females for all behaviour problems, but the difference was not significant for destructive behaviour. Intact males and neutered females were most likely to be presented for behaviour problems. There were more intact than neutered males in the catchment population, but more neutered than intact females.

Takeuchi *et al.* (2000) found that male dogs significantly outnumbered females in cases of destructive behaviour. In contrast, 117 dogs (61 males (52%), 56 females (48%)) with separation anxiety were examined at the Behaviour Clinic of the Veterinary Medical Teaching Hospital at the University of California during the same period. In the study from New York and in previous studies by Borchelt and Voith from Pennsylvania (Voith and Borchelt, 1996) and by Podberscek *et al.* (1999) from the UK, significantly more male dogs than females were examined because of separation problems, whereas Wright and Neselrote (1987) from Georgia found no sex difference. There may be an interaction between sex and climate, particularly if male dogs that display destructive behaviour indoors can be kept outdoors in warmer areas.

Candidate genes for canine misbehaviour

In the case of aggression, there are many candidate genes: monoamine oxidase A in humans (Brunner *et al.*, 1993) and mice (Cases *et al.*, 1995), serotonin 5-HT1B receptor in mice (Saudou *et al.*, 1994) and alpha-calmodulin-dependent protein kinase II (CaMKII) in mice. This enzyme is required for activation of tryptophan hydroxylase which is the rate limiting step in serotonin synthesis (New *et al.*, 1998). In humans, a genetic mutation in the gene for tryptophan hydroxylase is associated with aggression (Manuck *et al.*, 1999). Transgenic mice over-expressing transforming growth factor alpha (TGF α) are also aggressive, but the relation of this to neurotransmitter or brain lesions is unknown. Finally, nitric oxide is involved in neural events throughout the body and, as a result, affects aggression. Knockout mice, lacking the neural form of nitric oxide synthetase, are aggressive (Nelson *et al.*, 1995). Mutation of any of these genes could be responsible for aggression in dogs.

The first identification of a gene that appears to be related to canine behaviour was that by Niimi *et al.* (1999), who compared the D4 dopamine receptor gene, *D4DR*, of Golden Retrievers and Shiba Inu. More allelic variation was found for Shiba than for Golden Retrievers, but that may reflect the larger gene pool of the native Japanese breed than of the imported Golden Retrievers. The Shiba is more reactive and aggressive but less trainable and playful than the Golden Retriever according to the ratings of Hart and Hart (1985) and Tanabe *et al.* (1999); they have more of the long-D allele than the

Golden Retriever. Humans with longer repeats in the *D4DR* gene have higher scores in personality traits for novelty seeking.

Summary

The changes in behaviour with domestication have, in general, followed changes in anatomy such as dropped ears, curly tail and spotted coats. Classical canine behavioural genetics indicates low heritability of such traits as hunting. Working dog behaviour has been better characterized than that of pet dog behaviour. The effects of sex and breed on behaviour and behaviour problems have been quantified, but single gene causes of abnormal behaviour have not been identified. The rapid advances in genomics, however, encourage us to expect that dogs will be screened for the gene alleles associated with aggression, anxiety and compulsive behaviour in the next decade, just as they are screened now for alleles associated with retinal pathology.

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