SOME PRACTICAL SOLUTIONS TO WELFARE PROBLEMS IN DOG BREEDING

P D McGreevy and F W Nicholas[†]

Department of Animal Science, University of Sydney, NSW 2006, Australia

[†] Contact for correspondence and requests for reprints

Abstract   *Animal Welfare 1999, 8: 329-341*

This paper reviews the history of the establishment of dog breeds, summarizes current health and resultant welfare problems and makes some positive suggestions for their resolution. Some breed standards and selection practices run counter to the welfare interests of dogs, to the extent that some breeds are characterized by traits that may be difficult to defend on welfare grounds. Meanwhile, little selection pressure seems to be exerted on some traits that would improve animal welfare and produce dogs better suited to modern society. Unfortunately, the incidence of certain inherited defects in some breeds is unacceptably high, while the number of registered animals of certain breeds within some countries is so low as to make it almost impossible for breeders to avoid mating close relatives. There are several constructive ways to overcome these challenges. Breed associations can ensure that reduction of welfare problems is one of their major aims; they can review breed standards; they can embrace modern technology for animal identification and pedigree checking; they can allow the introduction of 'new' genetic material into closed stud-books; and they can encourage collaboration with geneticists in identifying and using DNA markers for the control of inherited disorders. There should be a concerted effort to produce and evaluate as companion animals first-cross (F1) hybrids from matings between various pairs of breeds. Finally, geneticists must learn to communicate their science better and in a language that non-geneticists can understand.

Keywords: *animal welfare, breeding, defects, dog, genetics, hybrids*

Introduction

While acknowledging the major contribution made by dog breeders and dog-breeding organizations in fulfilling the important need of humans for animal companions, breeders and scientists have long been aware that all is not well in the world of companion animal breeding. Welfare concerns associated with modern dog breeding have been discussed in the veterinary literature (eg Wegner [1979; 1995]; Peyer & Steiger [1998]) and the popular press (eg Lemonick & Smith [1995]). The aim of this paper is to review briefly the history of the establishment of breeds, summarize the present problems, and, most importantly, make some positive suggestions for overcoming them.

The early days

In the earliest days of domestication, dogs would have been selected for (among other things) the ability to interact favourably with humans, some aspects of which are known to be heritable (Goddard & Beilharz 1982; 1983; 1985). This is presumably what first allowed dogs to succeed in the human domain. Beyond being tame to humankind, early dogs had to work for a living; they could not be a burden on resources. Like most traits, hunting behaviours are heritable (Karjalainen *et al* 1996; Liinamo *et al* 1997; Schmutz & Schmutz 1998). It is not surprising, therefore, that humans selected dogs for hunting attributes, giving rise, for example, to the emergence of pointers that point and setters that set. The general-purpose hunting dog such as the Weimaraner is something of an exception, being a jack of all trades. Other strains of dog were selected to work as haulage animals, guardians of property and protectors of livestock.

Humans have gone to more effort in changing the body shape of dogs than of any other domesticated species. Athleticism was highly prized in the early days of the working breeds. For work in burrows, short, bowed legs were favoured. Skull shapes were also subject to change. The functional snout of the wild canid became widened to accommodate the powerful jaws of baiting dogs, while the nostrils became set back to allow the animal to breathe through its nose while biting.

Hence, most (if not all) of the traits subjected to selection in the early days of domestication had direct utility and functionality.

The formalization of breeding – impact of breed standards on trait functionality and dog welfare

Many of the traits for which there was initially a functional basis were incorporated into the breed standards when dogs left the working arena and entered the world of dog shows. Now it seems that some show standards place more importance on appearance than on functionality. Breeders compete with one another to see how well they can produce phenotypes that conform to a written standard – including traits that have, at best, questionable welfare benefits.

The following examples are taken from current breed standards[1]. The Pug, for example, should have eyes that are 'very large, globular in shape' (Kennel Club, London 1994; FCI Standard No 253). Is it a coincidence that Pugs have a tendency to present at veterinary clinics with exophthalmosis and exposure keratitis? For the British Bulldog, the 'skull should be very large – the larger the better' (Pre-1987 Kennel Club, London). This is a breed in which large foetal head size commonly leads to dystocia (difficulties in birthing). This same breed is also required to have curved 'roach' backs. It is perhaps not surprising that they are sometimes born with twisted spines, ie hemivertebrae. Finally, the requirement that in Dachshunds (Wire-haired), 'the whole trunk should be long' (Pre-1987 Kennel Club, London) is surely contributing to the prevalence of prolapsed intervertebral discs in this breed.

Sometimes breed standards are confusing, blurred and contradictory. For example, the Japanese Chin is required to have a head that is 'large in proportion to [the] size of dog, [a]

---

[1]   All the breed standards cited in this paper can be viewed on the Internet at: http://www.akc.org/bredgrp.htm and at http://www.rnswcc.org.au/breedlst.html. Sources of the standards are listed as the Kennel Club, London; the American Kennel Club; and/or the Federation Cynologique Internationale (FCI) – the (continental) European body.

broad skull, rounded in front, and between [the] ears, but never domed' (Kennel Club, London 1994). How can one achieve a broad skull, rounded in the front and between the ears, without being domed? Similarly, the Shar Pei (Kennel Club, London 1994; FCI Standard No 309) is required to have 'loose skin' and a 'frowning expression', but the 'function of the eyeball or lid [should] in no way [be] disturbed by surrounding skin, folds and hair', and dogs should be 'free from entropion' (rolled-in eyelids). In fact, the combination of loose skin and a frowning expression is likely to predispose to entropion. Furthermore, breed standards can affect temperament. For example, in a breed such as the Puli which should have 'long hair [that] overshadows [the] eyes like an umbrella' (Kennel Club, London 1987), simply cutting the hair that obstructs a dog's vision can improve its temperament (Houpt 1991). Interestingly, the same breed standard describes a temperament that is 'wary of strangers'.

Scott and Fuller (1965) argued that cranial morphology has a direct relationship with brain dysfunction. Citing post-mortem evidence of mild hydrocephaly in Cocker Spaniels (American), they conjectured that, 'in selecting for skull shape, the breeders accidentally selected for a brain defect'. The breed standard (American Kennel Club 1992; FCI Standard No 167) favours a skull that is 'rounded but not exaggerated with no tendency toward flatness; the eyebrows are clearly defined with a pronounced stop' (ie a pronounced junction between the nasal planum and frontal bone). The combination of roundness in the skull, definition in the brow and pronunciation of the stop must have contributed to an unhealthy skull shape.

In some cases, traits that are best regarded as defects have actually been included in breed standards. For example, brachiocephaly is prompted by the standard for the Boston Terrier (American Kennel Club 1990; FCI Standard No 140) that requires an animal to be 'short headed' and to possess a 'square head and jaw' with a muzzle that 'is short, square, wide and deep...shorter in length than in depth; not exceeding in length approximately one-third of the length of the skull'.

The fine legs of the Miniature Poodle and the Italian Greyhound are susceptible to fracture as a sequel to jumping. The unusual conformation of their radii relative to the mass of their bodies, increases the risk that these dogs will damage themselves while performing an innate behaviour (jumping).

Even the Australian native dog is under threat, with dog fanciers showing interest in having dingoes appear in shows (Lemonick & Smith 1995). How can we improve on animals that have succeeded in a hostile environment for thousands of years? The creation of a written breed standard for such animals, and its pursuit in the show ring, speaks of either considerable naivety or arrogance.

Selection for neoteny – hope and peril for dog breeding

The steady transition from wolf to dog has brought with it a reduction in the brain:body weight ratio – brain sizes in adult dogs are considerably smaller than in adult wolves of equivalent body weight (Coppinger & Schneider 1995). In equating this reduction in size with the arrest of brain development, Coppinger and Coppinger (1998) noted that reduced brain size is consistent with the retardation of foraging and hazard-avoidance behaviours, as seen in modern domestic dogs. Furthermore, modern dogs demonstrate a number of neonatal behaviours such as soliciting care, begging for food, and sitting around at a rendezvous point 'waiting for parents' (Coppinger & Schneider 1995).

Selection for what humans regard as desirable traits has repeatedly involved the retention of juvenile morphological and behavioural characteristics in adult examples of a breed. From a behavioural aspect, a number of features are worth noting. Dependence for food, care and leadership, readiness for play, acceptance of substitute objects to elicit hunting behaviour, or a relatively high tolerance for unfamiliar humans and conspecifics, are all juvenile traits that were selected when humans started to keep dogs as pets. Adult domestic dogs bark far more than their lupine counterparts. One possible explanation for this is that modern dogs have been selected to exhibit a behavioural neoteny that prevents them from wanting to be pack leader (Lorenz 1965) and makes them dependent on the pack for many of their activities. Despite this, we keep them on their own. Then we wonder why they vocalize when left alone. We have made them dependent and have then left them in isolation. The use of anti-bark collars in such dogs seems to represent a real threat to welfare.

As dogs made a transition from working to companion animals, selection for morphological neoteny found favour. This tendency is obvious among old and modern lap dogs. For example, with 'large dark round' eyes, pendant ears and 'compact, cushioned' feet, the Cavalier King Charles Spaniel (Kennel Club, London 1994; FCI Standard No 136) has a very puppy-like conformation. While this selection for neoteny or paedomorphism has strengthened the human-canine bond, it is also associated with attenuation of visual signalling and the behavioural repertoire in many breeds, as in the British Bulldog with its 'rose' ears that cannot be pricked up (Goodwin *et al* 1997). This may be associated with problems related to socialization. The welfare impact of reduced signalling capability has yet to be established.

Negative aspects of current breeding practices

Peripheral traits have now become important. Breeders often devote more energy to refining the quality and colour of their dogs' coats than to caring for the health of the wearers. Selecting for colour has resulted in some changes that can be extremely unwelcome. For example, there appears to be an association between coat colour and aggression in self-coloured Cocker Spaniels (Podberscek & Serpell 1996); and there is definitely an association between pigmentation and neurological defects, eg deafness and eye disorders in merle dogs, in which both homozygotes and heterozygotes are affected (Klinckmann *et al* 1986). Breeding for hypo-pigmentation is a questionable strategy.

As far as behaviour is concerned, motor patterns that are favoured can sometimes be overselected. This can give rise to compulsive tendencies, eg Border Collies have been selected to 'show eye' (stare) and many now demonstrate a fixed stare at blank walls. While self-narcotization (Dodman *et al* 1998) may mask the true extent of a welfare problem, such repetitive behaviours (sometimes termed stereotypies) can interfere with the animal's normal behavioural repertoire and, in extreme cases, prompt euthanasia (Overall 1997).

In other cases, selection for a combination of morphological traits has potentially compromised some of the standard means of canine communication. Old English Sheepdogs have difficulties raising their hackles (because of a hair coat that is too soft and long), displaying bared teeth (because of whiskers), delivering fixed stares (because of their veil), and wagging their (bob) tails.

We should be clear about the environment that most companion dogs occupy. The work for which many breeds were intended has all but disappeared, to be replaced by restricted exercise in inner cities. Their owners are often present for only brief parts of their life. A cynic might argue that there is a case to be made for selection favouring lower exercise

demands and a reduced predisposition to separation-related distress. However, selecting against separation-related distress could mean selecting for reduced dependence or even augmented self-confidence – leading to dominance problems for pet owners. Others might argue that owners who leave animals for long periods on a regular basis should not be owners at all.

Misdirected selection pressure?

After breeders have taken into account the many traits incorporated into breed standards, there is very little selection pressure remaining to be devoted to traits that are directly related to welfare and adaptability to modern (mainly urban) environments. If less attention were paid to traits of only peripheral importance, it would be possible to impose quite strong selection for relevant temperament and performance.

By performance, we are not referring to athletic performance. Breeds that are field-tested, eg the racing greyhound, have fewer orthopaedic problems than other breeds of similar size. It is a foolish punter who bets on an animal having assessed its worth in the parade ring alone. Why then do we persist in doing this with the other breeds?

The minimum performance requirement is the ability to survive birth without assistance. Where genes can be passed from one generation to the next only with the intervention of a veterinarian who performs a caesarean section to overcome relative foetal oversize, it can be argued that both dam and offspring have failed an essential performance test. Unfortunately, there appear to be no market forces to discourage canine caesarean births. On the contrary, it is common for both breeder and veterinarian to benefit financially from this practice, because the price of the surgery is passed onto the purchasers of the pups.

The problem of limited gene pools

Even without pressure from breed standards, many breeders would still find themselves producing dogs with serious defects. The reason for this has been known for a long time, but the practical implications are still not appreciated widely. As explained in Appendix 1, almost every animal that has ever lived has carried at least one deleterious recessive gene. The average number of deleterious recessive genes carried by an individual dog (or cat or horse or human) could be as high as 20. Lists of canine disorders known to be caused by deleterious genes have been published in various reviews, one of the more recent being in Robinson (1990), where 91 such disorders are listed. An on-line catalogue, which is maintained and regularly updated by one of the present authors (*On-line Mendelian Inheritance in Animals* [OMIA] at: http://www.angis.org.au/Databases/BIRX/omia/), includes more than 400 disorders that have been reported in dogs, of which 72 are definitely due to a deleterious gene at a single locus. (Because the data are often incomplete, opinions vary as to whether particular disorders are really single-locus or not.)

Each disorder brings with it different welfare concerns. Even those that are not life-threatening are still significant, ranging from the frustration of being less able to play due to respiratory problems in the case of brachiocephalics with compromised airways, to the stress of corrective surgery in dogs with orthopaedic problems. Many dogs are euthanased on humane grounds because their defects are deemed to compromise profoundly the quality of their lives. Not surprisingly, novel defects are reported from time to time, eg 'twitchiness' in miniature Wire-haired Dachshunds (Fitzmaurice & Shelton 1998), and some of these will turn out to be inherited. The present-day lists are just the tip of the iceberg!

Because deleterious genes are maintained by natural selection at a low frequency, the incidence of any particular defect is usually so low as to go without notice. However, the mating of relatives (inbreeding) changes this drastically. Inbreeding does not, on average, change the frequency of the deleterious genes, but it does dramatically change the frequency of genotypes. In particular, it increases the frequency of homozygotes, which has the effect of bringing those deleterious recessive genes out into the open, where their effects can be seen (for a more extensive discussion, see Nicholas [1996]). The take-home messages are obvious – that even the purest of pure-bred animals is likely to be carrying deleterious genes, and that the greater the level of inbreeding, the greater the chance of breeding dogs with inherited defects.

Given these undeniable facts of life, it is obvious that the aim of dog breeders should be to avoid the mating of close relatives. In numerically small breeds, however, this is almost impossible, because it is often extremely difficult to find a mating pair that does not share ancestors within a couple of generations. As an indication of the extent of this problem, 21 of the 174 breeds recorded with the Australian National Kennel Council (ANKC) had fewer than 20 new animals registered in Australia in 1998 (ANKC personal communication 1998; Table 1). How can breeders hope to avoid inbreeding with numbers as small as this?

To borrow a phrase from the late Professor I A Watson, a plant geneticist at the University of Sydney, these breeds are 'puddling in their own gene pools'. Their gene pools are so small that they have, in effect, no room to move; there is no choice but to mate close relatives, and hence to increase substantially the level of inbreeding, thereby increasing the prevalence of inherited disorders due to recessive genes.

Table 1   **Established breeds with fewer than 20 animals registered with the Australian National Kennel Council in 1998 (Australian National Kennel Council personal communication 1998).**

Breed	Numbers registered
English Toy Terrier [Black and Tan]	19
Dandie Dinmont Terrier	9
Sealyham Terrier	0
Norfolk Terrier	13
Norwich Terrier	2
Chesapeake Bay Retriever	12
Clumber Spaniel	17
Irish Red and White Setter	17
Italian Spinone	10
Large Munsterlander	17
Sussex Spaniel	1
Finnish Spitz	19
Bluetick Coonhound	0
Wire-haired Dachshund (Standard)	16
Harrier	0
Belgian Shepherd Dog (Laek)	0
Komondor	8
Polish Lowland Sheepdog	5
Swedish Valhund	17
Leonberger	5
Tibetan Mastiff	1

These same forces are acting in those breeds with larger numbers, but in general, the numerically larger the breed, the less severe will these problems be. However, even in those

breeds with very large numbers of registered animals, the tendency to concentrate on just a small number of families (often called 'line-breeding', which is just another word for inbreeding) means that the actual rate of inbreeding is often far higher than one would expect from the number of dogs registered.

The end result is that most breeds have their characteristic list of inherited defects, as documented by Patterson (1974; 1977), Foley *et al* (1979), Clark and Stainer (1983), and Kirk (1986). Some of these defects occur at an unacceptably high frequency. For example, Wilson disease (copper toxicosis) occurs with a prevalence of around 25 per cent in Bedlington Terriers in the UK (Herrtage *et al* 1987) and the USA (Yuzbasiyan-Gurkan *et al* 1997), and has been reported at a prevalence of as high as 46 per cent in the same breed in Holland (Ubbink *et al* 1998). Given that there is money to be made by treating these disorders, are there financial disincentives for veterinarians to be more active in controlling them?

All is not lost, however. With the increasing use of molecular technologies in investigations of inherited disorders, there is now a real promise of simple blood or hair tests that will enable carriers of undesirable genes to be identified (Holmes 1998). As shown by Kolosi and Gunn (1997), it should also be possible to establish international 'gene banks' comprising frozen semen from different populations of the same breed, and to use these 'banks' to overcome the restrictions imposed by small numbers of breeding stock in particular countries. Of course, reproductive technology such as artificial insemination can be misused – it can be used to spread the genes of a small number of animals widely throughout a breed, which will only exacerbate the inbreeding problem. However, if used as proposed by Kolosi and Gunn (1997), this same technology can be used to drastically reduce the level of inbreeding in a particular population, by providing breeders with a wider choice of animals with fewer ancestors in common with the local breeding stock.

Discussion
The challenges
From the preceding sections, it is evident that current breeding practices present five major problems:

   i) Some breed standards and some selection practices run counter to the welfare interests of dogs, to the extent that some breeds are characterized by traits that may be difficult to defend on welfare grounds.

  ii) Little selection pressure seems to be exerted on some traits that would improve animal welfare and produce dogs better suited to modern human living.

 iii) The incidence of certain inherited defects in some breeds is unacceptably high.

 iv) The number of registered animals of certain breeds within particular countries is so low as to make it almost impossible for breeders to avoid the mating of close relatives.

  v) There may be financial disincentives for veterinarians to reduce the incidence of inherited disease.

Possible solutions
There are several constructive ways to overcome these challenges.

   i) Breed associations and their umbrella organizations should ensure that the breeding of animals with fewer welfare problems is one of their major aims. A perusal of the *mission statements and objectives of a range of breed societies and umbrella* organizations in several continents has failed to identify any statement along these

lines. There is much talk about keeping pedigree records and maintaining breed standards, and sometimes there are statements about improving the quality of the breed. However, since these latter statements often sit alongside breed standards that are at variance with the welfare of dogs, there seems to be a strong argument for replacing the concept of quality with the concept of welfare.

ii) There should be a review of breed standards, with the aim of removing any aspects that could be contributing to welfare problems and/or encouraging breeders to waste valuable selection pressure on ephemeral traits; and replacing them with attributes that reflect the well-being of dogs in contemporary (mainly urban) environments. A very simple selection criterion could be the number of trips to the veterinarian, or the total veterinary bill.

On the behavioural front, a positive step would be to performance test breeding animals in homes. Interestingly, this is an argument against early desexing of pure-breds, a practice which tends to give the monopoly to breeders, and reduces the opportunities for dogs which show particularly good temperaments in family homes to be used as breeding stock. If the performance of animals in homes could be recorded and used as a basis of selection, the prevalence of unwelcome behaviours could be decreased over time.

iii) Breed associations and their umbrella organizations should embrace modern technology for animal identification and pedigree checking. Microchipping, which has no deleterious effects on animals, should be embraced to ensure correct identification of animals for performance recording and for other purposes, including showing. In addition, dog breeders should follow the lead of breeders of other domestic species such as horses and cattle, by embracing the use of DNA technology for pedigree checking. Correct identification and correct recording of pedigrees are essential means to the end of breeding better dogs.

iv) Breed associations and their umbrella organizations should provide leadership in identifying major inherited problems within breeds, and in collaborating with geneticists to identify and use DNA markers for the control of inherited disorders. Considerable progress has already been made in this area: at the time of writing, 17 inherited disorders have been characterized at the DNA level, and a tightly linked DNA marker has been identified for three other disorders (see Table 2). Certain breed societies have been instrumental in some of the research that led to these successes. However, much more needs to be done. In particular, financial support is required to bring the dog genome map to its full potential (for a recent report, see Mellersch et al [1997]), and to enable researchers to use this and other scientific resources to develop DNA tests for important inherited disorders. The necessary research procedures have been worked out. All that is needed now are funds to cover the costs, and blood samples from all members of families (both affected and non-affected) in which particular disorders occur.

v) Breed societies that are numerically small should be encouraged to cooperate internationally, to facilitate the movement of genes between countries. In some breeds, of course, international trade of breeding stock has been utilized extensively for many years. However, the breed societies that are in most need of this are likely to include breeders who do not have the resources for importation on their own. A

cooperative approach to international 'gene banks' could be very helpful in such circumstances.

vi) Breed societies' rules should be changed in order to allow the introduction of 'new' genetic material into a breed. There should be a provision for crossing between two breeds, and then back crossing to the desired breed. After only three or four generations of back crossing with selection, the resultant animals will, for all practical purposes, be indistinguishable from pure-bred members of the breed. Yet, they will have received a healthy 'dose' of new genes which could help to reduce the incidence of inherited disorders that are common in a breed, especially if there is strong selection against the disorders during the back crossing process. How difficult is it to introduce genes from outside a breed? At present, it seems to be nigh on impossible: the mainstream kennel clubs in the UK and USA, and the Australian National Kennel Council, appear to have no provision for the introduction of new genes – all breeding dogs must have pedigrees comprising only dogs registered in that breed. Breeders have no alternative but to 'puddle in their own gene pools'. This imposes an extreme limitation. As noted by Hancock (1995), some practical breeders have felt so strongly about the need for 'rescuing' breeds, that they have stepped outside the confines of the breed societies, and have created their own new 'breeds', based on back crossing programmes like that described above. That new named breeds are still being created (Hancock 1995) may not be such a bad thing, as long as their stud-books never close. The important point is that breeders should be encouraged to venture out of their own gene pools.

Table 2   **Canine disorders which have been characterized at the molecular (DNA) level, or for which there is a linked DNA marker.**

Mutation identified	Linked marker
Complement C3 deficiency	Narcolepsy
Fucosidosis, alpha	Rod-cone degeneration, progressive
Glycogen storage disease I	Wilson disease (copper toxicosis)
Glycogen storage disease VII	
Haemophilia B	
Krabbe disease	
Mucopolysaccharidosis I	
Mucopolysaccharidosis VII	
Muscular dystrophy, Duchenne and Becker types	
Nephritis, X-linked	
Pyruvate kinase deficiency of erythrocyte	
Rod-cone dysplasia-1	
Rod-cone dysplasia-3	
Severe combined immunodeficiency disease, X-linked	
Skeletal myopathy and dilated cardiomyopathy	
Tremor, X-linked	
Von Willebrand disease III	

Source: *On-line Mendelian Inheritance in Animals* (OMIA) http://www.angis.org.au/Databases/ BIRX/omia/. A complete list of references and some summaries of current knowledge about these disorders are available at this site.

vii) There should be a concerted effort to produce and evaluate first-cross (F1) hybrids from matings between various pairs of breeds. Contrary to popular belief, F1 hybrids between pairs of breeds are quite predictable in terms of morphology and

behaviour. Indeed, this predictability will be as great as, if not greater than, the predictability of pure-breds. However, being the combination of two breeds, such hybrids will have a far lower chance of exhibiting the disorders that are common within the parental breeds – their genetic health will be substantially higher. Furthermore, they will show hybrid vigour (heterosis) for a range of traits associated with viability. In addition, with such a wealth of pure-breds to choose from as parents in such a crossing scheme, it should be possible to find combinations that suit just about every human need, and match just about every type of modern environment in which dogs are likely to be kept. Once particularly favourable combinations have been determined, breeders of the parental breeds will have a large market for the sale of companion dogs. This highlights the very important point that, far from being a threat to pure-breeding, the sale of F1 hybrids could be the financial saviour of pure-breeders. There are already examples of the way in which F1 hybrids combine favourable traits from both parental breeds. The Labrador Retriever x Poodle (Labradoodle) has received attention from Australian guide dog associations (M Ponting personal communication 1999) because it combines the 'tolerance' of the Labrador Retriever with the hypoallergenic coat of the Poodle.

The lesson of crossing breeds to produce commercial offspring was learnt decades ago by pure-bred pig breeders, and during the last decade or so by pure-bred beef cattle breeders. In both cases, pure-breeders of the relevant breeds have successfully joined forces to advertise the virtue of the F1 hybrid between their particular breeds. Since the many advantages of crossing outlined here are seen only in F1 hybrids, breeders will be quite justified in dissuading people from using the F1 hybrids as breeders. Indeed, they could all be neutered before sale, thereby ensuring that other sorts of hybrids (which will be far less predictable) are not created, and, at the same time, providing a steady source of income for the pure-breeders. Under this scheme, therefore, everyone will benefit – the dog, the breeder and the owner. The authors of this paper would welcome suggestions on how an evaluation of hybrids could best be achieved in practice.

viii)Geneticists must learn to communicate their science better in a language that non-geneticists can understand; they must become an integral part of breed societies; they must provide educational programmes for breeders; and they must ensure that the public are well informed about the attributes of breeds and their crosses. Two key processes that can make so much difference are communication and education. As long as breeders believe that professional scientists 'have made genetics a foreign language' (Hancock 1998), misguided breeding programmes will persist. It is the responsibility of professional geneticists to make their messages available and accessible to breeders, so that informed decisions can be made. Similarly, when the potential puppy-buying public become more aware of the health problems that exist within each breed, market forces will exert their full effect and breeders will feel added pressure to avoid marketing unhealthy pups.

Animal welfare implications

The practical solutions suggested in the preceding sections have the potential to substantially improve the welfare of modern dogs. In a world that is beginning to appreciate the importance of biological diversity, it is appropriate that the animals bred to share our homes are as diverse as their owners and their owners' lifestyles. The environmental niche that

companion dogs fill is unprecedented in evolutionary terms. Just as their early ancestors had to be functional and appropriately behaved for successful domestication, so too should modern dogs be selected for these traits above all others. Breeders should acknowledge that many traditional showing and breeding practices are serious impediments to that process.

Acknowledgments

Appendix 1 (reprinted, with permission of the Scientific Program Committee for the 6th World Congress on Genetics Applied to Livestock Production, from Nicholas [1998].)

In a challenging paper that was published many years ago, Morley (1954) showed how theoretical population genetics can tell us lots of important things about the real world. The simplest case involves recessive lethals – which is what we will consider here. We start with the result first shown by Haldane (1927) and clearly explained in many textbooks (eg Falconer & Mackay [1996; pp 34-35]), namely that at equilibrium between mutation and selection, the frequency (q) of a lethal recessive gene at a locus is approximately the square root of the mutation rate at that locus. If we take the generally accepted figure of mutation rate as being approximately one in a million, this gives $q = 1/1000 = 0.001$, which in turn means that the frequency of the normal gene (p) is $1 - 0.001 = 0.999$. Now, the frequency of non-carriers at that locus is simply the square of the frequency of the normal gene, namely p^2, which equals $(0.999)^2 = 0.998$. This tells us the circumstances for just one locus. For two loci, the chance of an animal being a non-carrier at both loci is the product of the chance for each locus, ie $0.998 \times 0.998 = (0.998)^2$. It follows that the chance of an animal being a non-carrier at n loci is $(0.998)^n$. The next thing is to ask: how many loci are there in the genome of mammals? The answer is not known, but most people would put the figure at somewhere between 50 000 and 100 000. To be really conservative, let's assume that the above calculations apply to only, say, 10 000 loci. In other words, we are greatly underestimating the number of loci for which these arguments are likely to apply. The chance of an animal being a non-carrier at each of 10 000 loci is $(0.998)^{10\ 000} = 0.00000002$, which is so close to zero that it doesn't matter. In other words, almost every animal that has ever lived has been carrying at least one deleterious gene.

What is the average number of deleterious genes carried per animal? We can answer this question by noting from the previous paragraph that at each locus, the chance of an animal being a carrier is $2pq = 2(0.999)(0.001) = 0.002$ approximately. For 10 000 loci, therefore, the expected number of recessive lethal genes in an animal is $10\ 000 \times 0.002 = 20$.

Obviously, there are some assumptions in the above calculations. Readers are encouraged to alter the assumptions, and see what effect it has. For example, if you choose a lower number of loci or a lower mutation rate, the expected number of deleterious genes per animal is smaller. However, it turns out that for any realistic set of assumptions, you can't avoid coming up with a theoretical prediction that just about all animals are carrying at least one deleterious gene.

We can conclude that carriers of deleterious genes are the rule rather than the exception.

References

Clark R D and Stainer J R 1983 *Medical and Genetic Aspects of Purebred Dogs.* Veterinary Medicine Publishing Company: Edwardsville, USA

Coppinger R and Coppinger L 1998 Differences in the behaviour of dog breeds. In: Grandin T (ed) *Genetics and the Behaviour of Domestic Animals* pp 167-202. Academic Press: San Diego, USA

Coppinger R and Schneider R 1995 The evolution of working dog behaviour. In: Serpell J (ed) *The Domestic Dog: Its Evolution, Behaviour and Interactions with People* pp 21-47. Cambridge University Press: Cambridge, UK

Dodman N H, Schuster L, White S D, Court M H, Parker D and Dixon R 1998 Use of narcotic antagonists to modify stereotypic self-licking, self-chewing and scratching behaviours in dogs. *Journal of the American Veterinary Medical Association 193:* 815-819

Falconer D S and Mackay T F C 1996 *Introduction to Quantitative Genetics, 4th edition.* Longman: London, UK

Fitzmaurice S and Shelton G D 1998 'Twitchiness' in miniature wirehaired Dachshunds. *Veterinary Record 143:* 204

Foley C W, Lasley J F and Oswelier G D 1979 *Abnormalities of Companion Animals.* Iowa State University Press: Ames, USA

Goddard M E and Beilharz R G 1982 Genetic and environmental factors affecting the suitability of dogs as guide dogs for the blind. *Theoretical and Applied Genetics 62:* 97-102

Goddard M E and Beilharz R G 1983 Genetics of traits which determine the suitability of dogs as guide dogs for the blind. *Applied Animal Ethology 9:* 299-315

Goddard M E and Beilharz R G 1985 A multivariate analysis of the genetics of fearfulness in potential guide dogs. *Behaviour Genetics 15:* 69-89

Goodwin D, Bradshaw J W S and Wickens S M 1997 Paedomorphism affects visual signals of domestic dogs. *Animal Behaviour 53:* 297-304

Haldane J B S 1927 A mathematical theory of natural and artificial selection. Part V. Selection and mutation. *Proceedings of the Cambridge Philosophical Society* 23: 838-844

Hancock D 1995 This noble breed. *Country Life* (March 16): 34-37

Hancock D 1998 Breeding for the next millennium. *Dogs Monthly 16(8):* 10-13

Herrtage M E, Seymour C A, White R A S, Small G M and Wight D G D 1987 Inherited copper toxicosis in the Bedlington terrier: the prevalence in asymptomatic dogs. *Journal of Small Animal Practice 28:* 1141-1151

Holmes N G 1998 Canine genetic disease: the beginning of the end? *The Veterinary Journal* 155: 1-2

Houpt K A 1991 *Domestic Animal Behavior for Veterinarians and Animal Scientists.* Iowa State University Press: Ames, USA

Karjalainen L, Ojala M and Vilva V 1996 Environmental effects and genetic parameters for measurements of hunting performance in the Finnish Spitz. *Journal of Animal Breeding & Genetics – Zeitschrift für Tierzüchtung und Züchtungsbiologie* 113: 525-534

Kirk R W 1986 A catalogue of congenital and hereditary disorders of dogs (by breed). In *Current Veterinary Therapy. IX. Small Animal Practice* pp 1281-1285. W B Saunders: Philadelphia, USA

Klinckmann G, Koniszewski G and Wegner W 1986 Light microscopic investigations on the retinae of dogs carrying the merle factor. *Journal of Veterinary Medicine, Series A 33:* 674-688

Kolosi J and Gunn I M 1997 An international gene bank for guide dogs: organization, utilization and potential. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics 12:* 145-148

Lemonick M D and Smith R 1995 A terrible beauty. *Time* (23 January): 37-42

Liinamo A E, Karjalainen E, Ojala M and Vilva V 1997 Estimates of genetic parameters and environmental effects for measures of hunting performance in Finnish Hounds. *Journal of Animal Science* 75: 622-629

Lorenz K 1965 *Evolution and Modification of Behaviour.* University of Chicago Press: Chicago, USA

Mellersh C S, Langston A A, Acland G M, Fleming M A, Ray K, Wiegand N A, Francisco L V, Gibbs M, Aguirre G D and Ostrander E A 1997 A linkage map of the canine genome. *Genomics 46:* 326-336

Morley F H W 1954 The importance and genetic control of undesirable recessive genes in livestock. *Journal of the Australian Institute of Agricultural Science* 20:143-150

Nicholas F W 1996 *Introduction to Veterinary Genetics.* Oxford University Press: Oxford, UK

Nicholas F W 1998 International livestock breeding – implications of inherited diseases, and the risks and benefits for Australia. In: *Proceedings of the 6th World Congress on Genetics Applied to Production, Technology Transfer Field Day, 14 January 1998, Armidale, Australia* pp 40-45

On-line Mendelian Inheritance in Animals (OMIA). Department of Animal Science, University of Sydney, NSW, Australia. http://www.angis.org.au/Databases/BIRX/omia/

Overall K L 1997 *Clinical Behavioral Medicine for Small Animals.* Mosby: Missouri, USA

Patterson D F 1974 A catalogue of hereditary diseases of the dog. In: Kirk R W (ed) *Current Veterinary Therapy. V. Small Animal Practice* pp 61-75. W B Saunders: Philadelphia, USA

Patterson D F 1977 A catalogue of genetic disorders of the dog. In: Kirk R W (ed) *Current Veterinary Therapy. VI. Small Animal Practice* pp 73-88. W B Saunders: Philadelphia, USA

Peyer N and Steiger A 1998 The assessment of breed defects in dogs in relation to animal welfare. *Schweizer Archiv für Tierheilkunde 140:* 359-364

Podberscek A L and Serpell J A 1996 The English Cocker Spaniel: preliminary findings on aggressive behaviour. *Applied Animal Behaviour Science 47:* 75-89

Robinson R 1990 *Genetics for Dog Breeders, 2nd edition.* Pergamon Press: Oxford, UK

Schmutz S M and Schmutz J K 1998 Heritability estimates of behaviors associated with hunting in dogs. *Journal of Heredity 89:* 233-237

Scott J P and Fuller J L 1965 *Genetics and the Social Behaviour of the Dog.* University of Chicago Press: Chicago, USA

Ubbink G J, Vandebroek J, Hazewinkel H A W, Rothuizen J 1998 Cluster analysis of the genetic heterogeneity and disease distribution in purebred dog populations. *Veterinary Record 142:* 209-213

Yuzbasiyan-Gurkan V, Blanton S H, Cao Y Y, Ferguson P, Li J P, Venta P J, Brewer G J 1997 Linkage of a microsatellite marker to the canine copper toxicosis locus in Bedlington terriers. *American Journal of Veterinary Research 58:* 23-27

Wegner W 1979 Genetic deficiencies relevant to animal welfare in dogs and cats. *Tierärztliche Praxis 7:* 361-366

Wegner W 1995 The applicability of animal protection law for the prevention of crippling breeding methods. *Der Praktische Tierarzt 76:* 11