Population Genetics in Practice

Principles for the Breeder

ALTHOUGH THE SCIENTIFIC DISCIPLINE of population genetics has existed for the better part of a century, its penetration into the world of the dog breeder is only just beginning, despite its importance and relevance to that world. Often I have heard dog breeders wish for an understandable guide to practical dog breeding, drawn from the principles of population genetics -- a set of guidelines for dog breeders that would show the way to a healthier way of breeding than the harmful methods of inbreeding and selection now practised by the vast majority. As things stand with traditional dog breeding, the competitive struggle for individual excellence has harmful consequences for breed populations. What is needed is for breeders to think in population terms, to look at each breed genetically as a population and each breeder involved with that particular population as a conservator of that breed in partnership with others.

At the present time, after twelve or fifteen years of existence of the canine diversity movement, most available discussions of dog breeding as a discipline still recommend linebreeding (a euphemism for inbreeding), breeding only "the best to the best," together with stringent artificial selection and multiple screening for genetic diseases. That is still the old way. Those are the methods that brought genetic crisis to the world of purebred dogs in the first instance.

Two and a half years ago on the Canine Genetics email list, I asked whether we could not collaborate to write down a set of rules, guidelines or principles aimed at breeding according to the principle *"primum non nocere"* -- "above all, do no harm!" Although a few people acknowledged the desirability of such a document, we never managed to mount a thorough discussion of which principles should be included. In the end I drew up my own provisional list of principles for 21st-century dog breeding, which I never published as I never was able to put it into a final form that I thought adequate.

The release of the sensationalistic one-hour video entitled "Pedigree Dogs Exposed" commissioned for the B.B.C. has galvanised the discussion of 21st-century dog breeding somewhat, through the threat of repressive regulation from government and kennel club authorities and the advance of the "animal rights" agenda. Nevertheless the futile wrangling between advocates of inbreeding and diversity advocates still continues unabated on the email lists. One cannot help feeling that, although a certain level of awareness may have been raised, perhaps we have not yet really gone anywhere since the mid-1990s when Dr. John Armstrong made his pioneering efforts to raise questions of canine population genetics on the Internet.

Meanwhile the exigencies of the Seppala Siberian Sleddog Project (a Canadian bloodline conservation and breed development initiative under Ministry of Agriculture charter) required that I "wing it" as best I could, creating for purposes of the Project a coherent body of breeding practices for conservation and development of the Leonhard Seppala sleddog strain. Lacking time to make extensive research of other rare or developing breeds, I worked mostly from my own knowledge of population genetics, within the parameters of our evolving SSSD breed, with relatively little light shed on our problems by the practices of other breeders in similar situations.

Not every breed may be in a position for its breeders to do some of the things we do in the SSSD Project -- breeders of

Chinooks, for example, cannot avail themselves of landrace stock from the "country of origin" of their breed, both because the breed is synthetic in origin and because its original component canine strains are not completely known. With the strong caution, then, that not every single measure here recommended may be possible or appropriate for all other breeds, for every situation, or for any given breed other than the Seppala Siberian Sleddog, I offer for consideration the following guidelines drawn from my own limited knowledge and experience.

Please realise I do not say that you (as an individual dog breeder) must necessarily do any or all of the things discussed in the following paragraphs. Still less would I wish to see any such guidelines imposed by government as laws or regulations upon the dog breeding community; I do not feel that breeders can be coerced to breed healthier dogs. I do suggest that if you are concerned about inbreeding, inherited illnesses, and lack of genetic diversity, you might wish to consider implementing some of the following principles whose observance we have found useful in the Seppala Siberian Sleddog Project.

Maintain Balance of Sires and Dams

Breeders should make a great effort to maintain a reasonably equal numerical balance of sires and dams; it is unwise consistently to use fewer individual sires than dams. The so-called "popular sires" syndrome, in which a small number of elite show or trial winners sire grossly disproportionate numbers of progeny in a breed population, has received much discussion and attention. What may not be so well realised is that this selfsame syndrome is repeated in miniature in most kennels, where one or two of the "best" males cover all the bitches, sire all the litters. (How often has one heard it put forth, and not only by novices, that "the best males should sire all the litters!") Any significant imbalance between the number of sires and dams automatically restricts the effective breeding population. In order to avoid such needless reduction, just as many individual males as bitches should contribute to the population; this holds true whether we speak of the breed population as a whole, or of the population within a single kennel.

Eschew Incestuous Matings

As controversial as this advice may still be, I nevertheless advise the breeder to do no incest breeding whatsoever (even if you would rather call it "linebreeding" or inbreeding). Just about all purebred dog breeds demonstrate serious and sustained inbreeding when the full known pedigrees are considered. There is little excuse for inbreeding to be continued in the first four generations of pedigree if it can possibly be avoided. Matings of related individuals closer than cousins ought never to be contemplated unless that should become absolutely necessary to prevent loss of a rare bloodline. That means: (a) no brother/sister matings, (b) no father/daughter or mother/son matings, (c) no half-brother/half-sister matings (i.e., sire and dam share one parent in common), (d) no grandsire/granddaughter or grandson/granddam matings, (e) no uncle/niece or nephew/aunt matings. Why should a practice universally decried with respect to our own species be so common in dog breeding? The principles of genetics are the same no matter whether humans, dogs, or other species are considered.

That does not mean that first-cousin matings (sire and dam have different parents but the same grandparents) are okay or recommended, either; it is simply a case of having to draw the line somewhere, at a given degree of consanguinity, in order to say "anything closer than this is quite beyond the pale and should not even be considered." (Otherwise excuses will inevitably be found even for full-sib -- brother/sister -- matings.) If the available pedigree diversity within your own breed allows you to draw the line further out, so much the better.

Inbreeding cannot be practised with impunity, without consequences. Inbreeding depression may not be dramatically visible to most breeders, but that is only because it is subtle, incremental and widespread. It is a proven fact that longevity, reproductive success, and the immune system are all negatively affected by even "moderate" degrees of inbreeding. Survival fitness has already been compromised in many breeds. For breeders blindly to continue down the path to destruction whilst telling themselves that they are merely "fixing type and exposing undesirable recessives" is inexcusable.

Understand and Monitor Coefficient of Inbreeding

To avoid frankly incestuous matings within the first three generations of pedigree is not sufficient in and of itself. The Coefficient Of Inbreeding (COI) must also be monitored, preferably over ten generations of the known pedigree, with a view to keeping it as low as possible. To calculate COI over more than two or three generations requires the use of computer software such as CompuPed, Breeder's Assistant, BreedMate, FSpeed, etc., in conjunction with a reliable breed database. It

cannot be done easily or accurately without computer assistance; fortunately a good number of applications are available that meet the purpose.

These days every breeder should understand clearly what Coefficient of Inbreeding is and just what it tells us. Unfortunately that is still far from the case. Wright's Coefficient of Inbreeding (the only scientifically acceptable version, though there is at least one specious version in popular use) represents the statistical probability that the alleles contributed by sire and dam at any given gene locus will be identical by descent . It may also be regarded as the percentage of multi-allele genes that are likely to be homozygous by descent for a particular mating. Therefore COI is the principle measure of the degree of inbreeding and its effects on the genome.

To calculate a four to six generation COI only gives a false sense of security; usually such a COI fails to tell the whole story and the ten-generation COI will be found to be dramatically higher. Many popular writers, of whom Dr. Malcolm Willis is probably the best known, speak as apologists for inbreeding at one moment, at the next moment attempting to assure us that the average COI in most breeds is quite low. That is simply not the case. In the first place, a true average COI for an entire breed is not easy to determine. People assume that such things are known, but they are not, because the requisite research simply has not been performed. But the assertion that the COI in an "average pedigree" is something on the order of four to six percent is ludicrous, something that can be disproven readily by anyone with a breed database and one of the above mentioned pedigree software applications. The four to six percent contention, when examined, will usually be found to be supported by pedigrees of four or five generations only. Such calculations fail to take into account the background inbreeding inherent in the breeding history of every dog breed; ten generations is the generally accepted standard for comparison. In some breeds even ten generations may not tell the complete story and whole-pedigree COI will need to be examined before breeders can truly know where they stand.

Another specious argument often voiced is that "inbreeding should be defined as any mating in which the COI is higher than the overall average for the breed." This is an unscientific and somewhat circular definition. It is ridiculous on the face of it, as COI is not a static measurement but a dynamic one, a new story each time a new sire is mated to a new dam. As mentioned, the average for most breeds is not known. Moreover, distinctly different "average" levels may obtain in different sectors of some breeds (as, for example, show dogs, working dogs, and pet stock). In any case, inbreeding is never defined by reference to a population; it is always a function of the relationship between the sire and the dam of a litter or an individual. Inbreeding exists when genes held by both the sire and the dam of a litter are identical by descent. It is certainly a truism that all present-day dog breeds are "inbred," or, more accurately, that inbreeding has occurred consistently throughout their history. That is why we have acute problems with genetic diseases in our dogs. For that very reason, one of our major objectives ought to be to lower the average COI of every breed by reversing the inherent bias of our present system towards inbred matings. But to speak of an "inbred population" is at best shorthand. Inbreeding has meaning only with reference to a specific mating. It results in an increase in homozygosity (and a corresponding decrease in diversity) which is the permanent effect of the inbreeding.

In a purebred dog breed COI can hardly be too low; almost always it is far too high! It is safe to say that most breeders are totally unaware of their own dogs' Coefficients of Inbreeding. Ignorance is no excuse. COI is the best tool the breeder has to assist in the conservation of genetic diversity. Without it he stumbles in the dark down the slippery slope to canine genetic depletion.

Pay Attention to the Trend in COI

It is impossible to recommend an arbitrary figure for maximum allowable percentage COI, as the situation of each breed is likely to be different. Probably anything greater than 5% constitutes a threat to genetic health, yet to set the bar at 5% would be virtually impossible in many breeds. It is easy to point to specific individuals in numerous breeds with COIs of 70% or more, but in many breeds it would be a real challenge to discover examples of less than 5% COI. There are breeds in which breeders would have to make great efforts to obtain COIs as low as 20%; in at least a few breeds 20% would be alarmingly and needlessly high.

Breeders should at least endeavour to grasp what the average 10-generation COI level probably is for their breed, at any rate in bloodlines with which they are familiar, and to seek to keep their own breeding well below that level! Otherwise the COI will continue to increase indefinitely, steadily, year by year.

One should take care that the COI trend in one's own breeding is never upward, but always either downward or at worst neutral. This is done by averaging the individual COIs of sire and dam (add the sire's COI to the dam's COI and divide by two) and then comparing this average with the COI for the trial mating or litter that would result from mating those two individuals If the litter COI is higher than the average of the parents, then obviously you are increasing the overall level of

inbreeding by performing that mating; ordinarily the greater the positive disparity between the two figures, the more the mating should be deprecated. (This rule of thumb has distinct limitations, though. When a low-COI bloodline or a frank outcross is being integrated with an existing high-COI bloodline, it may still be quite desirable to perform matings in which the mating COI exceeds the parental average, since the end result will still be a desirable increase in diversity for the high-COI subject bloodline.) Conversely, a litter COI lower than the parental average is desirable. As far as I know, despite some claims to the contrary, there is no danger in an abrupt decrease in litter COI from parental levels.

You may also wish to look at the same data from a different perspective by calculating (with the same pedigree software) the Coefficient of Relationship (RC) when examining trial matings, the more easily to ascertain which of two or more alternative matings has the least-related parents.

Calculate Number of Unique Ancestors

A deep and reliable breed database, used in conjunction with a pedigree and COI application such as Breeder's Assistant or BreedMate, is a basic tool to explore COI and trial matings. That is far from its only use, though. The database and pedigree application should also be used to study the number of unique ancestors in the known pedigree. By that I mean the number of actual individual dogs showing in the full pedigree, as against the number theoretically possible in each generation; invariably the number of actual ancestors will be radically smaller than the number theoretically possible. Next you should determine the number of ancestors in common between sire and dam, and finally the number of ancestors unique to each parent. These figures are useful to assess the potential diversity of a projected mating and will tell you more than the simple COI (which, after all, is only a percentile probability figure predicting the likelihood that alleles at the same gene locus contributed by the sire and dam will be identical by descent). One of the best guides to the probable genetic diversity available in any particular mating is the number of ancestors not common to both parents. You will find that this tool dramatically points out genetically impoverished matings, and conversely that it easily isolates matings that are markedly superior from a diversity standpoint. This technique is one of the most valuable tools in actual practice, yet few make use of it.

Actual numbers of unique ancestors will vary from one breed to another, particularly in response to the depth of known pedigrees. It is of little use without a complete breed database; pedigrees in which some lines have not been researched beyond the usual four generations will distort results.

Know the Genetic Load but Don't Obsess About it

By "genetic load" we mean the total complement of genes within a population that can negatively affect the fitness of individual animals. Some of these genes are known; many remain poorly understood or unknown. The breeder should at least be well aware of genetic problem areas within the breed. Some will be breed-specific (syringomyelia in Cavalier King Charles Spaniels, the purine metabolism defect in Dalmatians); more will be common to most or all canine breeds (epilepsy, canine hip dysplasia) but in some breeds may be associated with particular bloodlines.

Breeders are told that to produce animals with genetic defects marks them as "bad breeders," so they tend not to share information about such defects. They are also told that their objective should be to "eliminate" these genes, which is used as justification for inbreeding and expensive screening programmes. This kind of advice builds up an obsessive attitude towards genetic load. People spend endless time discussing specific defects, individual animals, screening programmes and the like, whilst ignoring the true causes of genetic disease.

It is unlikely that canine genetic load can be effectively eliminated, at least at the present stage of genetic knowledge. Not until the functions and interactions of all genes in the dog genome are fully known, and gene surgery commonplace, would that become a real possibility.

It is therefore important that breeders share knowledge about genetic load within their breeds, so that they can avoid unfortunate breeding combinations. Authors such as Malcolm Willis and Jerold Bell insist that outbreeding "covers up" recessive defects. Indeed it does and indeed it should! That is exactly what nature itself does, and no one criticises natural evolutionary processes or recommends that natural populations should be inbred instead of mated naturally. The fact that inbreeding "exposes" recessives is not necessarily helpful, because in most cases it is impractical to remove or "eliminate" the "defect" genes. Rather, breeding should be guided in such a way as to avoid reinforcement of known recessives whilst maintaining genetic diversity in the population.

Screening and selection can never succeed as a strategy for the "elimination" of genetic disease. As one defect is

eliminated, others will be reinforced, and the latter state of the breed will be worse than the former. The genetic load must be known, tolerated and managed; to obsess about its elimination will lead only to disaster.

Use Pedigree Analysis

Every breeder should also carry out in-depth pedigree analysis for each prospective mating, listing the major ancestors on which inbreeding occurs in that mating, noting the number of occurrences and the generation number of each occurrence. This analysis should be carried back for at least six ancestral generations, ideally for eight. This practice will alert the breeder to undesirable "pile-ups" on key animals and therefore to potential genetic problems (where these are known to be associated with such individuals) in the planned mating. This can be done entirely without computer software. However, an alternative or supplementary approach is to use the "percentage blood" function of pedigree software such as Breeder's Assistant. The percentage blood function, in contrast to COI, illustrates just where in the pedigree major inbreeding problems may be occurring, whether just in a handful of key animals, or more broadly throughout the entire pedigree.

Conserve Sire and Dam-Line Diversity

There are two unique points of canine pedigree diversity that are not always paid much attention. These are the topmost and bottommost lines of the pedigree -- the tail-male or sire-line and the tail-female or dam-line. They represent unique genetic content, held by the mitochondrial DNA and the sex chromosomes, much of which is transmitted only by those pedigree lineages. Given the intense preoccupation among breeders with both stud dogs and brood bitches, what I am going to say may seem surprising: diversity in sire and dam lines is often quite scarce in purebred dog genomes.

In the case of the Siberian Husky (one of the breeds most familiar to me) there are two major founder sire-lines and two major founder dam-lines, along with perhaps one or two others that are well on the way to extinction. I have every reason to believe that most other breeds are in similar case, due largely to hazard, simple chance. Since these lines are not consistently scrutinised and conserved by breeders (because they are unknown if the breeder has not researched the pedigree all the way back to breed foundation), they are subject to changes in the frequency of their occurrences, exactly similar to the changes in gene frequency that occur due to random drift. Most breeds begin with a fair number of unique sire and dam lines. But some drift into prominence and others into obscurity, scarcity, and finally extinction.

These lines are important, particularly the dam-line with its association with mitochondrial DNA. This kind of DNA is held outside the cell's nucleus, in the cell mitochrondria within the cytoplasm. Since the spermatozoon has no mitochondria it plays no part in the transmission of mitochondrial DNA, which is inherited only from the dam. Mitochondrial DNA is directly involved in energy metabolism and is therefore vital to performance in working dogs.

The breeder should know the available unique sire and dam-lines in her breed and within her own kennel, and should make every effort to conserve them. That means ensuring that the sons of sires contribute to the next generation, likewise the daughters of dams. It is all too easy to neglect this vital point. Loss of tail-male and tail-female lines within kennels leads quickly to their loss within breed populations.

Practise Assortative Mating

If the breeder should wish to emphasise or fix greatly desired traits, she should consider the use of assortative mating (mating unrelated parents who are phenotypically similar for the desired traits) instead of inbreeding. Assortative mating is much less dangerous than inbreeding and will accomplish much the same ends. It should be obvious that to breed "like to like" for given desired traits will tend to yield more of what is desired, but if the parents are not closely related, there is a greatly reduced chance that other unconsidered traits will be unknowingly reinforced by such matings.

Maintain High Generation Time

Genetic losses occur infallibly with almost every generation of purebred dogs. This happens through a variety of causes -- random drift, from too few progeny contributing to the next generation, from the inbreeding/selection cycle, bottlenecking, etc.. For that reason, the fewer the intervening generations between foundation stock and current stock, the less genetic diversity is lost. Breeders should therefore maintain a high average generation time (age of the sire at mating plus the age of the dam at mating, divided by two) for each litter produced: four years should be considered an appropriate minimum

floor level, five or six is better. It is helpful to calculate a running average generation time for your kennel throughout its history, by keeping a grand average of the average generation times of all litters produced.

Far too little attention is paid to generation time by breeders. Many flagrantly disregard the question. How often have we seen the bragging advertisements in dog magazines: "CHAMPION (subject to CKC confirmation) Frou-Frou, finished from puppy classes at 10 months! Offered at stud to approved bitches only. Puppies from Ch. Frou-Frou are eagerly awaited next month!" The dog that is capable of finishing a title at ten months of age may turn out to be anything at all when mature; to mate such a dog at less than one year of age is breeding blindfolded. Often serious genetic diseases do not manifest until three or four years of age. To maintain a high average generation time gives the breeder a distinct advantage when it comes to producing healthy stock, and makes breeding results more predictable, as well as minimising generational losses of genetic diversity.

Avoid Repeat Breedings

Many kennels make a routine practice of repeating favourite breedings over and over again. Do not always use the same sire for a particular bitch (or vice-versa)! Take care to maintain diversity in your matings. Endless repetitions of the same matings greatly reduce the available breeding combinations both within the individual kennel as well as for the breed at large. This principle would seem quite obvious on the face of it, yet how many people ignore it as soon as they find a "nick"!

Ensure Sibling Contribution

The breeder should strive to ensure that at least two of every litter (unless it should happen to be one of those litters that really had best be forgotten) contribute to the next generation; half the litter should be the ideal, though perhaps a difficult one to maintain. In every instance in which only one progeny from a given mating contributes to the next generation, automatically and infallibly half of the available genetic diversity in that line is lost permanently! If two progeny contribute the theoretical average loss is reduced to 25%, still less if more littermates contribute. This single point is a major source of losses of genetic diversity among purebreds, yet it often goes totally unconsidered by the breeder.

Monitor Fitness Indicators

Breeders should not fail to monitor key indicators of survival fitness in their canine stock. These are nestling viability, absence of stillbirths, birth weights, fertility (percentage of successful matings), fecundity (average litter size compared to the norm for your breed), survival to adulthood, and longevity; be sure that your breeding programme does not trend toward the reduction of any of these.

Attempt Founder Balancing

It may be valuable to attempt to balance the relative contributions of founders (where possible and appropriate), particularly subsequent to founder events or genetic bottlenecks. This is routine practice in zoological park captive-breeding programmes, yet virtually unheard of in a canine context. "Founder" is a not an absolute, but rather a relative term. If a breed has a long pedigree history with original breed foundation stock at thirty or more generations remove from current stock, it may well prove impossible to balance the contributions of the original breed founders, whose relative contributions may already be set in stone for all practical purposes. But founder events tend to occur repeatedly within the history of a breed, not only when the stud book is first opened. Bottlenecks occur with dismal regularity. At least the breeder can pay attention to the most recent founder set that is clearly identifiable, attempt to prevent the loss of individual bloodlines that are seriously under-represented, and seek to balance the relative contributions. Clearly this is no simple matter and to suggest that it be applied consistently may be a counsel of perfection. At least it is one more possible tool in the breeder's armoury against diversity losses.

Consider Outcross Matings

The great majority of dog breeds have been bred within a completely closed studbook for sixty to a hundred years or

longer, with little or no fresh genetic input throughout the entire period from breed foundation to the present. In most cases the stud book was opened for a year or two, a small number of founders, often closely related to one another, were registered, and the stud book was then closed. Thereafter, only dogs descended from the founders could be registered. And for those sixty to a hundred or more years, artificial selection, random drift, bottlenecking and other forms of attrition took their toll of whatever genetic diversity was present in the founder group. It is exactly as though a bank account had been established with a single initial deposit (the genetic diversity of the founders), with no further deposits permitted; meanwhile bank fees and direct debits (diversity losses from drift, selection, etc.) chiselled away at the balance. It is a sure and certain recipe for bankruptcy.

Similarly, many individual bloodlines have been treated in exactly the same way, bred in relative genetic isolation from other bloodlines -- except that in this case additional deposits are at least allowed, in the form of bloodline outcrosses. Therefore each breeder probably ought to consider the desirability of locating and using a true outcross within his or her own breed (unrelated to one's own stock for at least ten to fifteen generations) at least once and to integrate the resulting progeny into one's kennel bloodline.

This cannot be done uncritically, outcrossing just for the sake of outcrossing. Some bloodlines might be an outcross to your own line, yet be worthless for the purpose. Generally, lines that come from the same ultimate foundation, but contain less diversity because they have been bred in a closed stud book for more generations, or have been heavily selected for cosmetic traits, will tend not to yield useful results.

If there is any possibility whatsoever to import unrelated stock from a breed's country of origin, one ought seriously to consider doing just that. This is mainly possible in the case of landrace breeds, in which an autochthonous regional population remains in the country of origin, independent of exported stock that may have become a registered breed in other countries. Examples of such situations would be the population of desert-bred coursing sighthounds in the Near East, relative to the Saluki breed in Europe and North America, or the relict populations of autochthonous arctic spitz-type sled dogs relative to the modern Siberian Husky, Alaskan Malamute, Samoyed, et al.

It would be difficult to overestimate the genetic value of a single import animal, unrelated to the registered breed population for scores of generations but stemming from exactly the same fountainhead. This I would term the Holy Grail of the diversity breeder -- the ideal controlled-outcross situation in which an immediate significant increase in healthy genetic diversity may be obtained at little to no cost in terms of breed type and purpose. (That the Canadian Kennel Club rejected this option for the Siberian Husky in 1994 demonstrates, I believe, the true extent to which the umbrella all-breed registries represent an obstacle to genetic health and true breed welfare and improvement.)

In cases of small, highly-inbred populations for which there is no landrace resource, it may become necessary to consider an outcross or outcrosses to similar breeds to relieve inbreeding depression and restore healthy genetic diversity. If so, this ought to be faced squarely and proactively by the breed club concerned and breeding subsequent to the breed outcross should probably be a collective endeavour, shared for purposes of more thorough integration and to reduce the work-load on any one breeder -- because, no question about it, the integration of a breed outcross is a major task that can hardly be undertaken alone by the average breeder. (The Backcross Project in the Dalmatian breed was an excellent example of a breed outcross well-purposed and superbly integrated; but the reaction of the breed club was deplorable.)

Monitor Population Growth

In the case of small, developing breed populations, it should be regarded as important to monitor and control the growth in number of the population such that there is steady expansion of the population within the limits of breeders' kennel capacity and the demand for progeny. Growth by fits and starts, with periods of rapid overexpansion followed by sudden cutbacks or population collapse, is very bad for genetic health. It is difficult to impossible wholly to avoid population bottlenecking, but its existence and ever-present threat should be recognised. To whatever extent may be possible, breed clubs and individual breeders should do what they can to ensure smooth, steady population expansion and to minimise cutbacks and consequent genetic bottlenecking.

Seek Balanced Traits

One ought always to evaluate breeding stock for balanced characteristics: health, vitality, temperament, working ability, intelligence, structure, type. Breeders should aim to maintain the balanced characteristics of a total dog, not just to produce winners at dog shows, field trials, races, etc. An all-round, balanced dog will be a much better hope for the future

than a highly-selected, over-bred animal thought to be "best" due to its possessing exaggerated traits in one or two areas, whether it be a "perfect head," a showy gait, a faster racing speed, or whatever. First, every individual needs to be a good dog, and that should come ahead of specialised breed considerations.

Avoid Unfit Breeding Stock

It ought not even to need saying -- but in these days in which extensive, heroic and expensive veterinary measures are routinely used to save otherwise doomed animals, it does need saying: the breeder ought never to breed from dogs that would not be alive but for such interventions (excepting, of course, survivors of physical injuries). It should be obvious that if we circumvent the operation of natural selection, many of the animals that we use for breeding purposes are likely to pass on various genetic weaknesses.

Avoid Reproductive Technology

Breeders should also consider whether it is in their breed's interest routinely to use elaborate reproductive technology to produce litters. These days various and sundry technical means are available which circumvent natural mating and whelping. Some breeds, indeed, cannot either mate or whelp a litter without veterinary intervention -- already! If we use artificial insemination and hormone assay to effect mating combinations that cannot be brought about by natural mating, along with routine C-section to deliver litters, we may rapidly find ourselves in the position of having created strains that cannot reproduce naturally without technological support. We should also consider whether it is really a good thing to freeze the semen of outstanding males and thus extend their breeding life decades into the future; this practice seems to be universally approved, while no one appears to have examined the effects such extension of the influence of individual stud dogs might have on breed genomes. If the "popular sire" syndrome constitutes a serious risk factor, frozen semen can only ramp up the risk level another notch.

Restrict Artificial Selection

Restriction of the use of artificial selection may really be the most important principle of all, and the most difficult for the vast majority to accept. Breeders really should avoid all extremes of artificial selection! When one comes to consider the problem of lost genetic diversity, inbreeding by itself is less than half the story. The hard truth is that breeders' selection itself is just as great a culprit, if not worse. Inbreeding and selection combine in a cyclical fashion in the dog world, to cause the systematic depletion ("depauperisation" to the geneticist) of purebred genomes. From the professional geneticist's standpoint, present-day purebred dog breeds are virtually all depauperate to a significant degree, therefore lowered in fitness, vulnerable to genetic disease and inbreeding depression. This situation is due to excessive artificial selection more than any other single factor.

When this goal is discussed most breeders react with dismay, asking "but how else can we set type?" If "type" has not already been "set" in breeds held within closed stud books for the better part of a century, then it never will be set. The truth is that selection is now used by dog breeders to create bizarre exaggerations of type, often unhealthy in themselves to the dogs. (Some examples, such as the nearly muzzle-less Pekingese, the respiration-challenged Bulldogs and the cerebrally-deformed Cavalier King Charles Spaniels, are already notorious in the dog world.) The desire for a cookie-cutter "consistency of type" causes healthy genetic diversity to be discarded intentionally at an alarming rate. (An example of this desire is the person who declared at a Chinook specialty show that he saw at least five different types represented there, and that "they had better get themselves a geneticist or they will never have a standard type." The Chinook is a working breed with a dangerously low population and a perilously narrow genetic base; the kind of diversity that engendered that comment is hardly to be deprecated in such circumstances.)

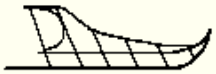
We hear endless discussion about inbreeding and its evils, and rightly so; yet we hear very little about the dangers of sustained extremes of artificial selection, which are if anything yet more dangerous than inbreeding. Together these two factors become an engine for the destruction of genetic diversity. People's constant obsession with having the "best" dog and with "breeding only the best to the best," whether in dog-show terms, in dogsled racing, or whatever, creates a situation in which the best is definitely the enemy of the good. The endless repetition of the inbreeding/selection cycle in the quest for a dog that is better than last year's best, has systematically stripped away most of the healthy genetic diversity from today's purebred dogs. Stringent, sustained selection for cosmetic ideals (shape, number and intensity of the Dalmatian's spots; shape and chiselling of the poodle's muzzle; subtleties of colour and markings in an endless series of

breeds) or narrow ideals of performance or athleticism (top sprinting speed in racing greyhounds or racing sleddogs) have for many decades taken absolute precedence over breeding to provide the kind of "genetic outfit" that will allow the dog to be healthy and hardy.

Now that canine diversity has been stripped to the point that homozygous recessive "defect" genes are everywhere apparent, the dog fancy proposes to remedy the situation by embarking upon a new level of elevated selection, armed with DNA marker testing to enable the wholesale "elimination" of "defective" genes. This new wave of super-selection on top of the already extant depauperisation may well become the killer wave that will sink the ship of purebred dogdom, AKC, CKC, and The Kennel Club with it. DNA testing has become a growth industry. This all may be more about corporate profits and grant money, than about canine genetic health. It is up to breeders to have the common sense to realise that what is being proposed is a losing game, that already depauperate purebred breed genomes will not support further massive artificial selection and the consequent wholesale elimination of yet more genetic diversity. The "defect" genes cannot be excised with a scalpel; many other genes that happen to reside on the same chromosomes will go right along with the defects, with totally unforeseeable consequences.

Conclusion

In conclusion, let me say that, although this set of guidelines cannot be made into hard and fast rules or (worse yet) regulations -- because the situations of each individual dog breed and even each breeder are different -- yet I believe we all need faithfully to attempt to apply such principles as those discussed above, in order that our dogs may have long, healthy lives upon the earth. We have made them whatever they are today; we are responsible for and to them. We should therefore strive to be faithful and responsible stewards of the genetic heritage of our canine friends. In that way we may hope that our bloodlines will endure longer in the dog world, and in the end we may even be remembered as pioneer 21st Century dog breeders who strove heroically to correct the errors of the past in the light of better knowledge of population genetics.



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Purebred Dog Breeds into the Twenty-First Century:

Achieving Genetic Health for Our Dogs

J. Jeffrey Bragg
Box 396
Rossburn, MB R0J
1V0
Canada

What is a Canine Breed?

WHAT IS A BREED? To put the question more precisely, what are the necessary conditions that enable us to say with conviction, "this group of animals constitutes a distinct breed?"

In the cynological world, three separate approaches combine to constitute canine breeds. Dogs are distinguished first by **ancestry**, all of the individuals descending from a particular founder group (and only from that group) being designated as a breed. Next they are distinguished by **purpose** or utility, some breeds existing for the purpose of hunting particular kinds of game, others for the performance of particular tasks in co-operation with their human masters, while yet others owe their existence simply to humankind's desire for animal companionship. Finally dogs are distinguished by **typology**, breed standards (whether written or unwritten) being used to describe and to recognise dogs of specific size, physical build, general appearance, shape of head, style of ears and tail, etc., which are said to be of the same breed owing to their similarity in the foregoing respects.

The preceding statements are both obvious and known to all breeders and fanciers of the canine species. Nevertheless a correct and full understanding of these simple truisms is vital to the proper functioning of the entire canine fancy and to the health and well-being of the animals which are the object of that fancy. It is my purpose in this brief to elucidate the interrelationship of the above three approaches, to demonstrate how distortions and misunderstandings of that interrelationship now threaten the health of all of our dogs and the very existence of the various canine breeds, and to propose reforms which will restore both balanced breed identity and genetic health to CKC breeds.

In order for canine breeds to fulfil their destinies effectively, the three distinct axes along which breeds are distinguished must have equal importance and consideration, otherwise serious problems arise. Breeds cannot be

distinguished by ancestry alone, by purpose alone, or by typology alone. Unless these three vectors of breed identity interrelate fully and co-operatively, the fulness of that identity is missing or marred. Unfortunately, this full and co-operative interrelationship is a rarity in our contemporary dog world. The criteria of ancestry are applied rigidly and mechanically; the criteria of purpose and utility are subordinated or not considered at all; the criteria of typology are applied in a highly exaggerated, obsessive fashion. The interaction of the three approaches is seldom considered and almost never is a sustained effort made at the integration of the three.

The Origins of Dog Breeds

CANINE BREEDS come into existence in many different ways and their beginnings are very often shrouded in obscurity. Let it not be thought that the three or four hundred-odd dog breeds now extant are the only ones possible, or that there cannot be any more truly new breeds. Such is the genetic plasticity of the dog that there is no end to the possible unique variations of which the species is capable. New breeds are born and old breeds die periodically. The genetic transformation of the dog goes on ceaselessly, and for that reason it is impossible that any breed should remain frozen, with all its characteristics fixed and unchanging, for any appreciable length of time. It must be realised that canine breeds are manmade, created by artificial selection out of the endless diversity of the canine gene pool. Breeds must not be confused with species or even subspecies, which occur naturally under the influence of natural selection; dog breeds are only unstable manmade varieties which would not survive unchanged in the natural world without human management.

An important characteristic of breeds is that they are created by breeders -- not by registries or protective organisations such as The Canadian Kennel Club. The origin and course of a canine breed is in the hands of its breeders, first, last and always. It is the business of cynological associations to facilitate and support the work of dog breeders and not vice versa. The purposes of the Animal Pedigree Act, under which CKC is incorporated, are the promotion of breed improvement and the protection of those who breed and purchase animals; such is the mandate of the Act and therefore of the Club (Animal Pedigree Act, Section 3(a,b)). All else is secondary.

Ordinarily a breed has already existed for an appreciable length of time before it reaches the point of becoming a recognised breed served by a registry. Nonetheless, the event of its "recognition" by a registry such as CKC is always a crucial one in the history of a breed. As things now stand, breed recognition is far more crucial (and ultimately damaging to the welfare of the animals) than it need be or ought to be, but more of that anon. First let us examine what is needed to start a new and unique canine breed.

FOUR ESSENTIAL CHARACTERISTICS usually distinguish the origin in the genetic sense of a new breed (as opposed to the discovery, popularisation and "recognition" of, for example, an autochthonous breed which may have existed in a particular region for a long time without connection to formal cynological structures). The first and most crucial characteristic is the **founder event**, in which a finite number of individual canines is chosen to contribute genetic material to found a new and unique canine population. They may all be quite similar, or they may be widely divergent one from another (as when Bulldog and Mastiff specimens were used to create the Bullmastiff breed). What matters is that a finite and sometimes quite small number of individuals are selected from the existing canine population and set apart so that their genetic material alone forms the gene pool for the new breed. That is in fact the next characteristic: **isolation**. If the founder group continues to exchange genetic material at random with the general canine population, a new breed will not result. Without genetic isolation of the new founder group, the differentiation that creates a new breed cannot take place. The logical consequence of this isolation is the next characteristic: **inbreeding**. If the founder group is of small or moderate size, such inbreeding cannot help but occur. Even if the founder group should be quite large, ordinarily those who guide the breeding which creates the new breed will find it necessary at some stage to employ a strong degree of incest breeding or inbreeding, to facilitate the weeding-out of undesired characteristics and the fixation of desired traits. Particularly if individuals of widely divergent type and physique are involved, inbreeding will be required to set up a stable genome in which random variability is kept within limits defined by the breeders. The final essential factor is **artificial selection**, since inbreeding alone will not serve to fix type characteristics and to eliminate unwanted traits. The breeders must select among the individuals produced in early generations so that only those displaying the desired characteristics are allowed to produce subsequent generations. Without the four factors of the founder event, isolation, inbreeding and artificial selection, new breeds ordinarily do not come into existence. These four tools are used to define a new genome which, hopefully, contains only the traits desired by the creators of the new breed and is able to reproduce itself, with its distinguishing characteristics, to a fair degree of stability and consistency.

The Healthy Continuation of Breeds

PUREBRED DOGDOM is even now in serious trouble through a general failure to distinguish between what is necessary to

establish a breed and what is desirable to continue that breed in perpetuity. Most registered breeds are less than a century old qua registered breeds; many are but fifty or sixty years old. Yet nearly all breeds now show levels of expression of genetic defects that must be considered unacceptable. Over 500 distinct genetic defects have been catalogued in various breeds of purebred dogs and more continue to come to light regularly. Some of these have reached very high levels of incidence, creating problems for breeders and dog owners, threatening the health of entire breed populations. What is worse, in many instances organised control programmes seem relatively ineffective. Although such programmes successfully identify affected animals, in some cases individuals with several generations of "clear" ancestry stubbornly continue to produce affected stock. Let us try to examine what has gone wrong and what must be done to correct the situation.

First of all it must be recognised that practices which were essential for the differentiation and establishment of a new breed may not necessarily be desirable for its continuation over time and may in fact be prejudicial to a breed's continued existence over the long term.

Let us take isolation, for example. Without genetic isolation, it would not be possible to control the genome of a new breed still few in number. It takes time and careful breeding to fix a new combination of characteristics; while that is being done, the regular addition of new genetic material would generally be counterproductive. Yet in the long term, if genetic isolation is maintained, it will necessarily lead to degeneration through genetic drift. Similarly inbreeding, if it continues to be practised after the need for it is past, will lead to a steadily increasing state of homozygosity which may well destroy the genetic health of the new breed. Even artificial selection, if carried on too strongly for too long, can combine with isolation and inbreeding to reduce drastically the effective breeding population, thus eroding the genetic health of the breed.

The Fallacy of Breed Purity

THE PRESENT STRUCTURE of The Canadian Kennel Club's studbook registry (and others like it) embodies a fallacy which is directly responsible for the current genetic crisis in purebred dogs: the fallacy of breed purity. The ideal of the purified lineage is seen as an end in itself; accordingly, the studbook has been structured to reflect and to enforce that ideal rigidly and absolutely. This insistence on absolute breed purity arises from nineteenth-century notions of the "superior strain" which were supposedly exemplified by human aristocracies and thoroughbred horses; this same ideal, pushed to an illogical conclusion on the human plane, resulted in the now discredited "scientific racism" of the Nazis, who tried through selective human matings to breed an Aryan superman. The idea of the superior strain was that by "breeding the best to the best," employing sustained inbreeding and selection for "superior" qualities, one would develop a bloodline superior in every way to the unrefined, base stock which was the best that nature could produce. Naturally the purified line must then be preserved from dilution and debasement by base-born stock. There is no support for this kind of racism in the findings of modern genetics -- in fact, quite the opposite: population groups that are numerically limited and closed to new genetic inflow are now thought practically certain to be genetically inferior. Certainly towards the close of the nineteenth century it became embarrassingly obvious that the human aristocracies of Europe were degenerating rapidly under their own version of the "closed studbook."

THE IDEAL OF BREED PURITY as applied to purebred dogs has resulted at the end of the twentieth century in a subculture that holds "purebred," registered animal stock to be qualitatively superior to crossbred or "mongrel" stock. (The word "mongrel" is in fact part of the vocabulary of racism, being applied equally to canine stock of no recognisable breed, to animal crossbreeds, and to persons of mixed race!) In this subculture -- presided over in Canada by the CKC -- it is thought to be of paramount importance that purebred stock be maintained unsullied by any genetic influence external to the supposedly superior strains that are produced by registered breeding in a closed studbook from a small group of foundation stock. New members of the CKC are required to subscribe to "Conditions of Membership" whereby they promise to have nothing to do with "dogs which are not purebred" (with the exception of family pets and boarders), "purebred" being specifically defined as referring only to dogs "registered individually or eligible for registration in records of the CKC." Litters which are made the subject of complaints that they may not be purebred are investigated and in many cases ceremoniously withdrawn from the registry by resolution of the Club's Board of Directors. Whether you like the word or not, this is effectively a special variety of racism in concept and in practice.

Not all dog breeders are in agreement with the proposition that breed purity is more important than anything else, particularly when they are confronted with the problem of breeding dogs to demanding performance standards. Mostly such dissenters are obliged to carry on their breeding without the benefit of centralised pedigree record keeping and official certificates of registration -- for example, those who breed "alaskan huskies," the high-performance racing sleddogs that dominate both short and long-distance dogsled racing, keep pedigree records and maintain sophisticated breeding programmes, but only as individual breeders. Yet sometimes even participants in established purebred registries engage in a subtle kind of rebellion, quietly breeding according to their own judgment in defiance of formal restrictions. Thus the Racing Greyhound Club of Australia, when it recently subjected a broad sample of stock from its registry to DNA testing, is

rumoured to have discovered that many pedigrees failed to match DNA ancestry findings and that considerable interbreed crossing had apparently occurred. Similarly most Siberian Husky fanciers are aware that some CKC bloodlines may have received surreptitious infusions of genetic material from non-purebreds or from other breeds. In some circles one even gets the distinct impression that "it's OK to crossbreed occasionally if you have a good reason for doing it and you manage it in such a way that no embarrassingly obvious mongrels are produced" -- i.e., "just don't get caught!" Thus the sanctity of breed purity may sometimes be less than inviolate in actual practice.

Population geneticists insist that limited populations under strong artificial selection, subjected to high levels of incest breeding -- such as our own CKC purebreds -- simply cannot maintain genetic viability and vigour in the long term without the periodic introduction of new and unrelated genetic material. They are referring, moreover, to true outcrossing, the introduction of stock unrelated to the breeding line, not merely the use of a dog which might be from someone else's kennel but is derived from exactly the same foundation stock some generations back.

The Demise of Typological Thinking

DNA RESEARCH has radically changed zoological concepts of species, subspecies and varieties. In the nineteenth century and the first half of this century it was thought that a species could be represented by a type specimen, that the vast majority of individuals of a species were virtual photocopies of the type specimen, genetically speaking, and that the genetic norm for most species was homozygous at most loci. In the mid-1960s the credibility of that idea was shattered as electrophoresis protein studies revealed extensive protein polymorphism that had not been previously suspected (Carson, 1983). Today the concept of a species in a satisfactory state of genetic health invokes a state of "dynamic balance" in which the species genome contains an array of genotypes with a high degree of heterozygosity, with multiple alleles at many gene loci. Natural selection is now thought to favour heterozygotes in a way which tends toward a high state of natural variability, preserving the greatest variety of possibilities with which a species can meet new environmental challenges. Conversely, species which have lost most of their genetic diversity, often through accidental population "bottlenecks" similar to those which regularly occur in purebred dogs, are held to be in high risk of extinction through the loss of adaptive capability. (The most notorious example is the cheetah, which is almost totally homozygous and is thought to have undergone at some time a bottleneck reducing its population to a tiny handful of specimens.)

There is no reason why dog breeds also cannot be maintained in a balanced state of heterozygosity, analogous to that of healthy wild animal species, if typological thinking in the dog fancy could somehow be replaced (or at least tempered) with population thinking. Fanciers will generally admit that no dog conforms perfectly to its breed standard. Thus the concept of the perfect type specimen, to which an entire breed ought to conform as closely as possible, is really as foreign to dog breeds as it is to animal species in the wild.

THE FANATICAL PURSUIT of breed type to the exclusion of other more important factors (more important to the dog, to his owner, and to his veterinarian) has led to a distinctly unhealthy situation in most breeds. Since the majority of breeders within CKC seem to direct their efforts toward the production of a winning exhibition specimen, and since many breeders therefore breed their females to the males that do the most winning at dog shows, a situation has arisen in which continued effort to produce show winners leads consistently to greater and greater exaggerations of "type," that being the factor most susceptible to the off-the-cuff three-minute analysis of the breed ring. It is an accepted fact that strong incest breeding is the fastest route to this kind of "success"; here is one successful show breeder's recipe for "excellence" (de Boer and de Boer, *DOGS in Canada*, April 1994):

> "My approach would be to identify an outstanding, dominant stud dog. Let's call him 'Shadrack.' To improve the odds, I'd buy or lease three bitches whose grandsire on the dam's side was the same as Shadrack's sire. Let's call the grandsire 'Fashion Hint.' I would breed the Fashion Hint bitches to Shadrack.
>
> "Assume, in this first generation, that I get three nice bitches. For the second generation, I'd breed them to a half-brother of these three bitches (Shadrack's son, also a dominant sire). For the third generation, several 'mix and match' options include going back to Fashion Hint or Shadrack. I could also do brother-to-sister or father-to-daughter breeding."

Thus the quest for more and more refined breed type leads directly to a state of advanced homozygosity, rising inbreeding coefficient, low effective breeding population and consequent impoverishment of the gene pool in most CKC breeds, through rampant uncontrolled incest breeding.

THE SHOW RING has also been largely responsible for the decline of breed purpose, working ability and temperament in a great many breeds, notably sporting breeds, herding breeds and sleddog breeds. The quick and easy gratification of blue

ribbons and gilt trophies all too readily supplants the hard work necessary to preserve and advance canine working abilities. If our dog breeds are to conform to the ideal of "a sound mind in a sound body" (as advocated by the proponents of the Advanced Registry), the fancy must find some way of ensuring that less dog-breeding takes place along the lines of least resistance and cheap gratification, so that greater attention is paid to working characteristics, temperament and trainability. A balanced outlook on breed identity must be restored by integrating canine function with the ideals of conformation, beauty and "type." All kinds of dogs, toy breeds not excepted, can perform useful functions and respond to training. Those aspects of the fancy should be accorded an importance at least fully equal to that of type and conformation instead of being regarded as merely optional. For example, breeding and exhibition of utility breeds such as gundogs and sleddogs merely for sale as pets and for dog shows, with no effort made to maintain and advance their working capabilities, is an obvious abuse which must lead inevitably to mental and physical degeneracy in those breeds.

Abandoning Natural Selection

THE BREEDER of domestic stock often assumes that he has abandoned the realm of natural selection and that only artificial selection plays a significant role in his breeding programme. Nothing could be further from the truth. The breeder may attempt to abandon natural selection; natural selection, however, will not abandon his stock. As one geneticist puts it:

> . . . Man-imposed characteristics, however, like the flower colours and forms selected by the plant breeder, usually do not perturb the deep-set genetic variability systems of the species. Most such changes are reversible when a less restricted gene pool is restored. The 'balance' system appears to be retained by natural selection, which, perhaps paradoxically, pervades most systems of artificial selection.
>
> --Hampton L. Carson, *The Genetics of the Founder Effect*, 1983

Those who attempt to set aside the balanced genomes arrived at by natural selection must struggle thereafter to attain and to maintain fitness in their stock. There is more to this than mouthing platitudes about "soundness." Artificial selection alone, such as that used to produce winning exhibition dogs, involves breeding in a way which flagrantly disregards most of the gene loci in the canine genome. Since genes assort in groups on chromosomes (a phenomenon known as "linkage"), inbreeding and selection for desired traits of superficial appearance unavoidably affect many other genes which are inadvertently selected and often fixed in a homozygous state in total ignorance of what is happening. This may be a major factor in the current prevalence of genetic diseases. Thus natural selection, baulked for a season by artificial selection, high-level nutrition, and advanced veterinary care, reasserts its primacy at a deeper and more serious level when the new genome as set up by the breeder proves flawed through genetic unsoundness, so that healthy and hardy animals can no longer be produced, however typey and attractive to the eyes of the judges the result may be.

Declining vigour caused by the inadvertent fixation of sublethal and subvital alleles will not be made up for by breed points. Fitness criteria may not be replaced with impunity by aesthetic criteria. The animal's environment is the ultimate arbiter of its fitness and will not be denied its say. You may vaccinate the dog and dose him with antibiotics, feed him with vitamins and minerals as you like, enclose him in a sterile pathogen-free laboratory environment if it comes to that! Still natural selection may not be avoided; it only emerges at a deeper level. In a sense the dog's environment includes his own physical body; if the genes which blueprint his physiology are flawed, then the dog is doomed regardless of his beauty and classic breed type. The truth is that the "superior strain" cannot be produced by manmade breeding programmes and artificial selection; the breeder's decisions are subject to nature's veto at all times.

WITH WHAT, THEN, will the breeder replace natural selection? If he replaces it with profit, the degeneracy of his stock will in the end put him out of business as veterinary costs and death eat up his profit margin. If he replaces it with beauty contests, in the end his beautiful contest winners will engender weaklings and degenerates. If he replaces with screening programmes for the "elimination of genetic defects," in the end his stock will succumb to inbreeding depression as bitches fail to whelp naturally and puppies die in the nest. If he replaces it with veterinary care, in the end his stock will die prematurely of incurable cancer, or the young will fall prey to viral diseases despite repeated polyvalent vaccinations. If he replaces it with work and austerity, his stock may endure awhile longer, but in the end it will turn out to be afflicted with genetic ills that slipped through his demanding programme, or its performance will mysteriously decline as the inbreeding coefficient creeps upward. In the end, natural selection cannot truly be replaced with artificial criteria. The breeder must find a way to work with natural selection, within the framework of what is now known about the biological operation of the natural world. We in the canine fancy must begin to take lessons from wildlife biologists, from evolutionary biologists, from population geneticists.

In our quest for breed purity, the superior strain, and classic type, we have made a sad mess of our dogs -- with unhappy, neurotic temperaments, epilepsy, blindness, deafness, immune system weakness, skin diseases, blood disorders, endocrine system malfunctions, crippling bone disorders, deliberate deformity, and often even the inability to reproduce

their kind without breeder and veterinary intervention. How clever we have been!

Can we not now take a clear-sighted view, as the millennium turns slowly over, of what we have done -- of our own pitifully-flawed creation in our world of purebred dogs and, like mature, intelligent people, clear away the mess and try to do better? Can we not learn from bad experience? If we would be truly clever, we might attempt to imitate more closely the methods of nature, to work within the natural system, albeit for our own ends. That would indeed be clever. I think that that is now possible, if we would but step outside our own incestuous little purebred world and learn something of what people working in other zoological fields of endeavour have already learnt.

A Century of Nineteenth-Century Dog Breeding

HOW, THEN, may we set about correcting the accumulated errors of over a century of what we might call nineteenth-century dog breeding? First of all it might be wise to attempt a short-list cataloguing the errors and abuses of which we are aware, the areas known to be deficient in one way or another.

• Dog shows must come high on the list. They began as an arena for the evaluation of breeding stock, they continued in the form of the "bench show" as a public showcase for purebred dogs. Both functions are now ill-served if not virtually abandoned. Championship shows are now just that, mills for the production of Champions, Best in Show and Group winners, little more. They contribute almost nothing to the true welfare of dog breeds; they have few lasting positive values to offer breeders, only ephemeral fads and fashions.

• Breed purpose and the cultivation of canine utility have a low status in the fancy, compared to what one author called "the glitz and hype of the show world." Those who concern themselves with the working ability of their dogs exist mostly in ghettos where little communication takes place with other branches of the fancy.

• Obedience work, begun as a way of initiating dog owners into the fascination and technique of training one's pet to be a pleasant, well-behaved companion, has become largely ritualised and sterile. The pursuit of "Club 200" (the perfect point score) has become an obsession. Intelligent and useful training on the owner's part, intelligent obedience on the dog's part, are now beside the point. What matters all too frequently now is the minutely-perfect performance of a set ritual. Here again we find a canine ghetto.

• The worship and exaggeration of type, as already noted, is responsible for a multitude of ills.

• Modern registries based on a rigidly-closed studbook are throttling the genetic health of all registered dog breeds. Genetic impoverishment is now a real and present threat. Many breeds now bear a genetic load of defects which has grown totally unmanageable as their respective gene pools have become more and more narrow through imprudent breeding and selection practices.

• Incest breeding, once a convenient tool for the rapid fixation of type in newly-registered breeds, has become virtually standard practice for those who seek success in dog breeding. The net effect has been the decimation of gene pools, widespread homozygosity and the unintended fixation of unknown scores, hundreds or thousands of alleles, many of which are proving to be harmful or lethal to the animals that bear them.

• The CKC, born in the height of the Victorian era, seems to cling to cumbersome structures, making it difficult for the Club to respond in a timely fashion to external challenges or internal needs. The entire By-Law and Amendment structure could do with modernisation. Many members feel there is little justification for such practices (for example) as the three-year member apprenticeship proviso, under which new members (or old ones who for whatever reason have let their membership lapse for a year or more) are completely disenfranchised for anywhere from three to five-plus years (inasmuch as elections and referenda are triennial), costing the Club dearly in lost members and wasted talent. Many members also feel that Board of Directors initiatives are frequently arbitrary and undertaken hastily with insufficient grass-roots consultation, while initiatives from the general membership must go through a slow and cumbersome multi-stage routine before they can be acted upon. One feels a general atmosphere within the Club of elitism and ultra-conservatism, as if those in power felt that only they themselves, the "old hands," knew what is good for purebred dogs and the fancy, and that newer members should not be entrusted with the franchise.

• Breed clubs seem to possess little real power to represent breeders or their breeds effectively. Special measures which they may feel essential for the health, development, and protection of the breeds whose breeders they represent must be put through the centralist CKC system and approved by the Board before they become effective; often such measures have little chance of approval because they are felt to conflict with the rigid all-breed norms of the Club. Since breed clubs have relatively little real power, they often tend to be less than fully representative of all breeders of a particular breed.

Frequently they are more or less run by cliques; they waste much time and effort in wrangling and personalities, being perhaps inadequately supervised and not taken terribly seriously.

• Breeders, as well, are sometimes far from free to make their own responsible decisions for the best interests of their own dogs and bloodlines, being closely constrained by CKC By-laws and by the Animal Pedigree Act. Little discretion is given them regarding matters such as the withholding of registration papers, delaying registration of stock until it reaches physical maturity, the introduction of new genetic material when in their judgment it is needed for genetic health, etc.

MANY OF THE ABUSES and deficiencies not rooted in outmoded attitudes such as racism and elitism arise from misunderstandings of genetic realities. Let us now examine briefly a few points of up-to-date genetic theory as they relate to purebred dog populations.

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Lessons from Population Genetics

Gene Frequencies

Much of the work of population genetics involves estimating or calculating gene frequencies, which quantify the relative commonness or scarcity, within a particular population, of alleles at a particular gene locus. If there is only one version of a gene in the population, then the entire population is necessarily homozygous for that gene. Gene frequencies are expressed as decimal fractions which must add up to unity, so a gene without alternative alleles has a frequency of 1.0. The gene frequency figure is a ratio of the number of copies of alternate versions of a gene in the population, independent of the number of animals involved and of whether they have the gene in homozygous or heterozygous form. An individual may have two copies of the same allele or it may have one or none. For example, if a locus has two alleles, and the population involved consists of fifty animals, and there are 25 copies of one allele, then the frequency for that allele is 0.25; therefore the frequency of the other allele must be 0.75, with 75 copies of it in the same population. It must be emphasised that gene frequency by itself says nothing about relative heterozygosity or homozygosity; it deals only with quantitative aspects of alleles in the population, not the diploid genotype of individuals.

Founder Events

Perhaps the most crucial concept in population genetics for dog-breeders is the founder event, for its theory describes perfectly what takes place when a breed is "recognised" by CKC or a similar registry. Whatever may be the state of genetic balance or the frequency with which particular alleles are found in the general canine population, it all changes when a founder event occurs. In nature such events happen when individuals of a species occupy and reproduce in territory new to the species, losing contact with the source population of the migrants (as when small birds are deposited by hurricane winds on mid-ocean islands). The founder event describes the establishing of a small population, although later on it may grow to be a large one. When a finite number of individuals found a new population group, the genome of the new group will necessarily reflect the genes brought to it by the founder animals; gene frequencies within that population will reflect the gene frequencies within the founder group rather than that of the source population. In this way, when a founder event occurs, a gene quite rare in the source population may have a much higher frequency in the new population; conversely, genes common in the source population may be infrequent or even absent from the new population. It all depends on the genes of the founders! Thus a genetic defect extremely rare in the overall canine population can come to be common in a particular breed simply because one or more individuals of a small breed foundation carried that gene.

Hardy-Weinberg Principle

The Hardy-Weinberg Principle states that under certain specific conditions (random mating, very large population group, no mutations, absence of selection pressure, for example), the relative allele frequencies of genes at a given locus will not change from generation to generation and can be described by an equation, allowing the geneticist to create a mathematical model of gene frequencies within the population. Without trying to explain the equation and its operation here, we can still say in general that the net result is that heterozygote organisms will be much more numerous than homozygotes in a Hardy-Weinberg population. Many natural populations can be described in this way, although purebred dog populations cannot, since they are subject to inbreeding, artificial selection, non-random mating and small populations.

Nonetheless, the principle has a certain significance, in that the overwhelming preponderance of heterozygotes in natural populations means natural selection tends to favour the heterozygote. Thus the natural genetic balance systems of most species include a high degree of heterozygosity (Carson, 1983). When we as dog breeders use incest breeding and artificial selection to fix characteristics arbitrarily, we are therefore quite likely to upset the natural genetic balance of the canine species in our breed populations. Moreover, the natural preponderance of heterozygotes is rendered even more important by overdominance effects, described below.

Genetic Drift

Small populations, such as most purebred dog breeds, are subject to a condition known as genetic drift. This is a situation in which gene frequencies change at random from generation to generation, varying from statistical expectations because of sampling error. (Sampling error occurs when too small a number of trials departs from the expectations of probability, as when someone flips a coin six times and gets five heads and one tail -- if he flipped it 600 times, the results would be close to 300 heads, 300 tails, but in a small sample, chance can cause a departure from the expected result.) This happens also when gametes unite to form zygotes in reproduction; the union of gametes is at random, by hazard. A dominant black dog, whose dam was white, when bred to a white bitch should in theory produce equal numbers of white and black pups, but few breeders would be very surprised to see 2 whites and 6 blacks, or vice versa. Yet when such sampling errors occur in small populations, over subsequent generations gene frequencies can change, taking a random walk that leads finally to the loss of one allele and the fixation of the other! The smaller the population, the fewer generations this result is likely to take. In a very large population, it will not happen at all. Genes are lost and other genes fixed completely at random in this way by genetic drift.

Generation Time

Since in limited, genetically isolated populations such as CKC breeds a certain amount of genetic diversity is lost with each reproductive event, through the action of genetic drift, inbreeding and artificial selection, the number of generations from the founder event becomes an issue. The average time between one generation and the next is a convenient yardstick to help us realise the relative rate of genetic attrition. A few instances exist in which certain bloodlines -- working dogs, usually -- are bred conservatively enough that the generation time is as much as an average six or seven years, but this appears to be exceptional. Many exhibition lines seem to operate on the following model: "Phoo-Phoo" starts his show career at six months of age in Junior Puppy class, is heavily "campaigned" and has all his Championship points by ten months of age. The owners' immediate "bragging ad" in "DOGS in Canada" or the breed club newsletter recounts his triumph, adding that "puppies from Ch. (subject to CKC confirmation) Phoo-Phoo are eagerly awaited next month!" In such lines the average generation time may be two years or even less. This reproductive rush has two implications: first, a greatly accelerated rate of loss of genetic diversity; second, an implicit selection for early maturity which carries with it an elevated risk of joint disease and a lowering of average longevity.

Effective Breeding Population

The population figure that matters in situations such as random genetic drift is not the total number of individuals alive at any one time. Nor is it even, as one might think, the actual number of individuals that contribute progeny to the next generation. Variations in breeding population from one generation to the next have a marked effect, such that the effective breeding population, especially where variations in number are extreme, tends to be only modestly greater than the lowest number. Another factor which makes a great difference and is crucially important in purebred animals is the sex ratio of successful reproductors. The effective breeding population can never be greater than four times the number of males, no matter how numerous the females may be, since gametes must come from both sexes. Thus anything that limits the number of males in use drastically restricts the effective breeding population. Overuse of popular sires is a tremendous factor in the genetic impoverishment of purebred dogs. One of the major drawbacks of the proposed CKC Advanced Registry is the virtual certainty that the existence and promotion of a few "elite" sires, titled, temperament-tested, and certified "clear" of major hereditary diseases, will further dramatically reduce the effective breeding population in many breeds, causing further declines in breed vitality and viability and leading to the loss of vitally-needed breeding lines which happen not to be among the elite group.

Linkage Disequilibrium

Genes found on the same chromosome will fail to assort independently in accordance with Mendelian principles. Such genes are said to be in a state of linkage disequilibrium. This simple fact has a devastating effect in artificial selection, since it means in practice that when a breeder selects for or against any single-gene trait whatever, whether he is aware of the fact or not he is also selecting for or against every other gene located on the same chromosome! This is how genetic

defects become rapidly fixed in inbred populations subjected to artificial selection. Since dogs have only 78 chromosomes (diploid number) but many many thousands of genes, obviously linkage disequilibrium can be tremendously influential. Genes that are linked eventually become unlinked over time (except in certain special situations) through crossing over, a process whereby chromosome pairs exchange segments of their DNA structure during meiosis. The unlinking process, however, is slow and unpredictable; it offers little hope of remedying the linkage disequilibrium problem in a few generations and of course is no help at all where deleterious alleles have already become fixed.

Overdominance

Situations exist in which a heterozygote individual enjoys a survival advantage over both the recessive homozygote and the dominant homozygote of the same gene; this is called overdominance or heterozygote superiority. As yet not much seems to be known about this mechanism and proven examples of specific overdominant genes are rare. Nonetheless this mechanism may be one reason (apart from their usually recessive nature) why genetic defects are persistently found in genomes despite their apparent fitness disadvantage in the homozygous state.

While on this subject it is worth noting that population genetics offers mathematical models for various forms of selective breeding, including the selective elimination of individuals bearing homozygous recessive genes for harmful traits. These models demonstrate that the elimination from the breeding population of individuals homozygous for unwanted traits has only the smallest effect in changing the allele frequency! It has been calculated, for example, that to reduce the expression of the recessive albino gene in humans from one in ten thousand to one in one million, simply by prohibiting albino (i.e. homozygote) individuals from having children, would require nine hundred generations of such selective breeding to accomplish! This is one of several reasons why screening programmes, although perhaps profitable for the veterinary profession, are of questionable effectiveness, since they identify only affected (usually homozygous) individuals.

Heterosis

More commonly known as hybrid vigour, heterosis is a situation in which a cross of two or sometimes three highly-inbred bloodlines displays enhanced performance for some desired trait, as for example higher yield in corn. It works best in plant species capable of self-fertilisation, but has been amply demonstrated in domestic livestock species. It is worth noting that in practice many different inbred lines must be developed at the same time, that most of the inbred lines become so unfit that they must be discarded as they become non-viable, and that considerable random trial of different crosses must be done to establish which lines will actually yield the desired result. Although the seed-grower's methods are unsuited to purebred dogs, the overall principle is of interest, since it is thought that heterosis works because of the heterozygosity of the hybrid generation, probably through the action of both dominant and overdominant genes. Geneticists are now starting to realise that the balanced-heterozygote systems of many wild species involve a heterosis effect which gives them a high degree of fitness.

Inbreeding Depression

As genetic variability diminishes and homozygosity rises through inbreeding, a syndrome known as inbreeding depression sets in. It is characterised by a reduction in viability (survival of individual progeny), birth weight, fecundity (number of young) and fertility (reproductive success), among other things. Much of it is caused by the homozygous presence of rare, deleterious recessive alleles. Part of it may also be due to the relative absence of overdominant heterozygote combinations. As inbreeding depression becomes more severe, highly inbred lines tend to become extinct through the loss of ability to reproduce successfully and/or inability of the young to survive. It varies somewhat in intensity from species to species, due probably to variations in the number and nature of lethal, sublethal and subvital alleles involved. Some wild mammals which show almost no juvenile mortality when bred in captivity without inbreeding, exhibit 100 percent juvenile mortality when inbred! A survey of captive breeding records for 44 species (Ralls and Ballou, 1979, 1982) showed that juvenile mortality of inbred young was higher than that of noninbred young in 41 of the 44 species for which records were analysed.

Genetic Load

The difference between the fittest genotype of a population and the average fitness of that population is known as genetic load. (Muller, 1950) It is, of course, caused by the presence of lethal, sublethal and subvital alleles. The more such alleles found in a population, the greater the genetic load. Genetic load is sometimes measured by the number of lethal equivalents, and the severity of inbreeding depression can be quantified in this way. Humans in general normally carry in a heterozygous state from 5 to 8 lethal equivalents per person -- genes or combinations of genes any one of which, if homozygous, would cause the death of the organism. It should be emphasised that genetic load is present in every population, since never are all individuals maximally fit. The presence of lethal, sublethal and subvital genes is a normal

state of affairs in all species. Homozygotes for such genes are usually so infrequent as to have little effect on species fitness. It is only when founder events and inbreeding occur that the gene frequency of deleterious alleles rises and genetic defects start to become a problem as the growing genetic load degrades the fitness of the inbred, limited population. Thus in the case of purebred dogs the problem does not inhere in the presence of "defect" genes, but in the registry and breeding practices of the purebred dog fancy!

Balanced Heterozygous Population Structure

In recent decades growing evidence from DNA studies of protein polymorphism conclusively disproved the "classical" view of species as being homozygous at most loci, with the phenotypes of all individuals of a species conforming to that of a type specimen. Population geneticists and evolutionary biologists now realise that typological concepts are useless in a natural world in which populations may best be described genetically not as individuals conforming to a type but as arrays of genetic variability. Some of the implications of the "balance view" are elucidated by one geneticist as follows:

> Species that are diploid and cross-fertilised *(this includes all mammals, Ed.)*. . . characteristically carry large stores of genetic variability in a balanced state in their populations. . . .
>
> Genetic recombination naturally generates diverse genetic types from the large field of variability in the gene pool. In order to meet environmental challenges, natural selection in many such organisms tends to develop a system based on the higher fitness of heterozygotes. These are maintained under regimes of selection that exploit the advantages of heterozygosity for many alleles simultaneously. In these, the large amount of genetic variability is continually being recombined as balanced hybrid vigour is maximised. . . .
>
> The genetic system is not a fixed and frozen entity but is dynamic and variable. . .
>
> By its very nature, this genetic system is inimical to the perpetuation of sameness. At each reproductive event an enormous field of genetic variability is produced. Most of the variability is held in sexual populations by a complex balancing selection based on the superiority of fitness of heterozygotes. . . .
>
> The biological conserver, short of putting the DNA into liquid nitrogen, cannot hope to freeze the characteristics of any natural population, be it a deme *(local population, Ed.)*, a subspecies, or a species.
>
> --Hampton L. Carson, The Genetics of the Founder Effect, 1983

Efforts at artificial selection and breeding which attempt to defy this system of balanced heterozygosity and variability will almost certainly fall foul of the kind of difficulties we are now encountering in purebred dog breeds. It is hopeless to attempt to freeze the genetic characteristics of small populations and even the attempt, which is doomed to eventual failure, is quite costly in terms of the loss of hardiness and viability. Artificially selected populations, too, can and should be maintained in a state of dynamic heterozygous balance. Thus the entire problem of genetic defects would be minimised.

Assortative Mating

Assortative mating is a method of selective breeding capable of creating homozygosity for desired traits without having as great an effect on overall homozygosity as does inbreeding. It consists of mating phenotypically similar individuals that are not closely related. This method of selective breeding would be capable of maintaining a reasonable range of breed type in a balanced-heterozygosity breed system with an open studbook.

HAVING NOW ACQUIRED a few of the more crucial concepts of population genetics, we are prepared to examine in a new light the nineteenth-century system of dog breeding and registration which we have inherited. As we prepare to enter the twenty-first century, perhaps we can conceive a renewed system which will serve our dogs and their breeders far better than the present one.

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Part Three: Renewing the System

Purebred Dog Breeds into the Twenty-first Century: Achieving Genetic Health for Our Dogs

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The Crux of the Problem

AS WE FACE the millennium, the one problem which most concerns the entire purebred dog fancy is genetic defects. Breeders used to worry about overshot/undershot bite and cryptorchidism. Not much else of a genetic nature was cause for concern; fanciers were a lot more worried about distemper, hepatitis and internal parasites. Breeding programmes concentrated on individuals' visions of canine excellence. Then in the 1960s the tip of the genetic iceberg emerged as concern grew about a joint disorder called hip dysplasia. A control programme involving the examination of hip x-rays by a skilled scrutineer and the maintenance of a registry of animals "cleared" of the defect was established at the Ontario Veterinary College at Guelph, Ontario. Now after three decades of the OVC programme it has been pretty well established that "clear" animals with several generations of "clear" ancestry can nonetheless produce dysplastic progeny (Chidiac-Storimans 1995)! Hence the OVC control programme would seem to be of questionable effectiveness. As the generations of closed-studbook breeding have advanced, a panoply of other inherited problems has emerged in purebred dog breeds. There is no need to list them here; the list would be on its way to obsolescence in a month or so; veterinary research continues to define more inherited disorders regularly. Many breeders now run four-way screening programmes; some may screen for even more problems. Many breeders' selection programmes for various kinds of canine excellence must now be at a standstill -- all the selection is going into the effort to produce stock "clear" for eyes, hips, elbows, blood disorders, endocrine dysfunction, etc. Yet thirty years of x-rays have not eliminated hip dysplasia -- it is now widespread in breeds in which it was not a problem thirty years ago.

In December 1994 "Time" magazine published a scathing indictment of the American Kennel Club and of purebred dogs and their breeders, targeting in a cover story the problem of genetic ills, suggesting that the best use of pedigree papers was for housebreaking the puppies and recommending that the public satisfy its desire for canine companionship with mongrels. Since then, most of us have known we have an untenable situation on our hands. Our reputation as breeders of purebreds is now in tatters; we are caricatured in the media as greedy, uncaring producers of degenerate animals. The CKC's main response to the situation was a Board policy statement that "reputable breeders will provide a detailed written guarantee of the present and future good health of the dog and will not hesitate to uphold their guarantees." The policy statement, far from helping the situation, only saddled breeders officially with a heavy responsibility without enacting measures which might assist them in living up to it.

nbsp; It is time for us as dog breeders to stand up for ourselves and for our dogs, to reject the imputation that we ourselves are individually to blame for the problem of genetic defects, and to demand swift remedial action by the Club and, if necessary, Agriculture Canada. The crux of the problem is the closed studbook and with it, the ideal of breed purity, the worship of type, and the pre-eminence of the championship show as goal and arbiter of most breeding programmes. Armed with the concepts of population genetics, we can now examine the last century of nineteenth-century dog breeding, ascertain what has gone wrong, and establish ways and means to correct the situation.

EARLIER WE STATED that the recognition of a breed by a registry was a crucial event in its history, more crucial than it need be. That is because the usual practice has been to open the registry to foundation stock for a limited period, to inspect and register a small population of foundation animals, and then to close the registry to new genetic inflow forever after, with the sole exception of animals of the same breed imported from other registries and derived from the same or closely-related foundation stock. In recent decades there has usually been no unique Canadian foundation stock except in the case of indigenous breeds; CKC merely accepts registered stock from other jurisdictions. (Actually the relationship of CKC foundation stock to that of other registries has never been clearly defined, so far as I know. CKC accepts registration papers of other studbooks which it considers to be "reliable." So long as the export pedigree shows three generations of registered, numbered ancestry; import stock seems to be eligible for CKC status without question. The criteria involved are clerical, not genetic.) Most of the breeds we are familiar with were founded from sixty to over one hundred years ago. In those days Canada's population was much smaller than it is now; the canine population was correspondingly smaller, too. Thus the number of dogs accepted during the open-registry periods was rather limited.

The canine species possesses tremendous genetic diversity as a whole. Like most species, that diversity includes a genetic load, a wide variety of more or less deleterious alleles, probably quite a few of them held in a state of heterozygote superiority, so that although natural selection tends to eliminate homozygote recessives when they segregate, the bad alleles themselves maintain a strong presence due to the selective advantage of the superior heterozygote. What happens when a founder event occurs? Then it is possible that bad alleles, uncommon in the canine population as a whole, may achieve a much higher frequency of occurrence owing to their presence in a small founder population -- especially since the foundation stock of a newly-recognised breed will already be considerably inbred from the breed development process. Inbreeding and selection together raise homozygosity levels dramatically through the wholesale elimination of alleles from the genome. Those alleles may be unwanted by the creators of a new breed; nevertheless their elimination raises the allele frequency of whatever remains.

An Example from One Breed

THUS THE RECOGNITION of a breed creates a founder event when the registry is opened; a limited number of breed foundation animals are selected, often from a population which has already undergone considerable inbreeding and selection. Let us take for an example the Siberian Husky breed. Registered in 1939, the initial CKC population consisted of 47 animals, all belonging to or bred by one kennel! Of those 47, nine were foundation stock of the kennel whose dogs were registered. Two of those were males imported from Siberia -- littermate brothers! The other seven were mostly related to one another. (Two were seven-eighths Siberian and one-eighth Malamute.) The other thirty-eight were all progeny and grand-progeny of the founders. Of the nine foundation animals, two were not bred from at all. Two were mated -- once only -- to each other: one only of their progeny contributed to further breeding. Of the two Siberia import males, one brother was always bred to the same bitch, producing a large number of progeny of identical pedigree; the other brother was usually bred to daughters of the first brother. Today, Siberian Husky lines that trace directly back to the Canadian foundation stock owe 25% of their pedigree lines to the first brother, 15% to the second brother, and 27% to the first brother's invariable mate! Two-thirds of the genetic heritage of these modern Siberian Huskies derives from only three foundation animals! This is not an exceptional situation, it is a fair example of the early breeding history of CKC breeds.

In the case of the Siberian Husky, then, (which happens to be my breed, with whose early history I am reasonably well familiar), The Canadian Kennel Club opened a registry in 1939, inspected one kennel's dogs and admitted four dozen closely-related individuals to the registry, which was then closed permanently. No effort was made to ensure a broad foundation, nor a numerous one, nor a genetically diverse one.

Just how permanently the registry was closed I recently found out when I imported from Russia a dog bred to the Siberian Husky standard! The dog was born in the Ural Mountains well within the boundaries of Siberia, from parents of Chukotkan village origins; he had three generations of known ancestry (without registration numbers since there is no official "Siberian Husky" registry in Russia). I was immediately told that the Club "did not know what to do" about my application to register the dog, that the protocols used to register breed foundation animals in 1939 were no longer valid, and that my dog "should not be used for breeding because it would probably be a long process," in spite of the fact that the dog had a valid FCI Export Pedigree from the Czech Republic (through which he was exported). A year and a half later after repeated in camera discussions, the import was refused recognition by the Board and Registration Committee on grounds of inadequate information (no ancestral registration numbers). Repeated calls for Club inspection of the import and offers to submit the animal to DNA tests and progeny testing were ignored. The registry is closed -- even to new Siberia imports!

For the past fifty-six years, then, all Siberian Huskies bred in Canada have stemmed from the 1939 registrations, or from American imports, which mostly stem from the same dogs CKC registered, plus perhaps three additional animals. The original foundation animals were poorly utilised and subsequent generations were so closely inbred that the two Siberia

import males plus one bitch are even today still statistically equivalent to grandparents of every single Siberian now registered!

Thus the original founder event in my breed plus the closed studbook has resulted in a state of forced inbreeding for Siberian Huskies. There is no such thing as an outcross mating in Siberians in any genetically meaningful sense. A sire can be found, perhaps, who may have no ancestors in common with a bitch for the last 5 or 6 generations -- if one knows all Siberian bloodlines well enough and doesn't mind going a few thousand miles to find him -- but he will not be an outcross, because all of his ancestors and all of the bitch's ancestors are the same animals, once the pedigree is taken back far enough. It would be difficult to calculate inbreeding coefficients for fifteen to thirty generations of ancestry; software to handle calculations of that nature doesn't seem to be generally available to breeders. (After all, a thirty-generation pedigree would contain over two billion names...)

THIRTY GENERATIONS of breeding all going back to ten dogs or fewer represents an impressive feat of sustained inbreeding! Predictably enough, Siberian Huskies, which eighty-five years ago were probably the toughest, hardiest variety of dogs on earth, now suffer from the same gamut of genetic defects that afflicts other breeds. Few if any registered Siberians are now able to perform as sleddogs on anything approaching the level of the 1910 dogs imported from Siberia. Probably this is mostly due to the decline in heterozygosity and loss of vitality through inbreeding. What is worse, unmistakable signs of inbreeding depression are surfacing in the breed: rising numbers of Caesarean births, smaller litters, lower birth weights, delicate nestlings prone to infection, etc.

Breeders of domestic livestock -- cattle, poultry, sheep -- manage to run registries and maintain breed type without imposing the concept of absolute breed purity. They inbreed to fix desirable traits, as do dog breeders. Livestock breeders, however, do not try to pretend that they can inbreed forever without ill effects. Thus when inbreeding depression or genetic defects threaten, they outcross -- repeatedly, if necessary. They can do so because they do not have closed studbooks. I do not suggest that we slavishly copy the procedures and registry structures of livestock associations, because I think they, too, might benefit from some restructuring in the light of modern genetic knowledge. Nonetheless I would make the point that we in the canine fancy are in a minority when we cling to absolute ideals of breed purity and insist on rigidly closed studbooks.

AS A DRAMATIC CONTRAST to the foregoing example of the CKC's Siberian Husky breed foundation, let us examine for a moment the standards which Agriculture Canada now applies to new domestic animal breeds in this country, as set forth in a three-page leaflet entitled "Establishment of a New Breed of Animals in Canada." Agriculture Canada now requires that breed foundation stock (that is to say, the first generation of registered animals of a new breed) be selected from the third filial generation (F3) or later of the "evolving breed" which precedes the actual, registered new breed. It lays down no parameters for the founder generation of the evolving breed, but it does state:

> The standard used for the creation of a new breed is as follows:
>
> - Minimum number of animals to constitute the foundation stock of the new breed (F3): 200 animals (unique genotypes).
>
> - In order to reach the required 200 F3 animals and in order to provide a sufficiently wide genetic base, it is recommended that the minimum number of animals to be produced in each F level be:
>
> F1: 60 animals
> F2: 100 animals

It also stipulates that "the F3 generation is the earliest generation to become eligible for inspection as foundation stock . . . In practice most evolving breeds will evolve over many generations before having developed a significant population of foundation animals."

These modern standards are at least somewhat influenced by population genetics considerations, in an attempt to establish a basis for genetic health and stability for new animal breeds in Canada. Yet in all probability very few of our existing CKC dog breeds, which are arguably of much greater economic importance than any new breed, would come anywhere near to the foundation stock now enforced by Agriculture Canada. The sole exceptions would probably be breeds, like the Canadian Eskimo Dog, accepted for registration during the last decade or two. As for the Siberian Husky, its actual genetic founders (those whose genes contributed to future generations, leaving aside those which did not reproduce) numbered 6 only; the F1 generation which actually reproduced numbered 8 individuals; the F2 generation which actually reproduced numbered just 5 animals; no F3 animals were registered in the first year of CKC registrations -- original founders, F1s and F2s were all registered together in the first year.

Thus it is obvious that the Siberian Husky, at least, could not begin to satisfy current Agriculture Canada standards for an appropriate number and variety of foundation stock to establish a new breed, when traced to its historic foundation. In all probability, few CKC breeds could do so. Yet the registry norms that are rigidly enforced by CKC, backed up by

Agriculture Canada, make the acceptance into the studbook of badly-needed new foundation stock a complete impossibility! Presumably Agriculture Canada has good and sufficient reasons justifying its standard for new breeds -- that being the case, then it is a curiously irrational situation that older, existing registered breeds not only are exempt from any such standard, but are actually prohibited from enlarging their founder group through the acceptance of unrelated primitive stock.

The Holistic Breed

NOW I WOULD LIKE to evoke a vision of the future -- but not the distant future. I want to describe how dog breeds might be in the twenty-first century. Instead of all breeds being subjected to arbitrary structures not equally well-suited to them all, each breed would get whatever special measures its breeders thought necessary. Instead of a fragmented canine fancy with ghettos of show fanciers, obedience buffs, and working-dog specialists, dog breeds would have the benefit of a holistic outlook, integrating the various aspects of canine activity and producing well-rounded, versatile, mentally stable animals. Let me stress that the suggestions which follow will be fully practical and down-to-earth. They involve no technology we don't already possess. They require no knowledge that isn't already generally available. All that is needed is a proactive attitude and the will to make necessary changes in an obsolescent structure. This vision could become a reality within ten years' time.

At the beginning of this brief I stated that the three distinct axes along which breeds are distinguished -- ancestry, purpose, and typology -- had to relate fully and co-operatively, or the fulness of breed identity would be missing or marred. Let me now describe how such a relationship might be achieved.

To begin with, we absolutely must open CKC studbooks, in every breed, to new genetic inflow. There can be no long-term genetic health in small populations such as our registered breeds without the periodic infusion of new genetic material. The one big "sacrifice" we shall have to make, if it is really a sacrifice, is to abandon racist attitudes and the concept of rigorous breed purity. We must recognise that first of all, a dog is a dog, species *Canis familiaris*, and that is his true identity. He is a dog first, before he is a Siberian Husky or a Foxhound or a Doberman; breed identity is subordinate to species identity. We must stop treating breeds as if they were species, abandon the rigidity and narrow typological thinking which has heretofore characterised the canine fancy. We must recognise that dogs are unique individuals and that there is no positive value in trying to create groups of dogs which are all clones or photocopies of a type specimen represented by a breed standard. This should not be too hard, since breeders and judges have never been able to arrive at agreed and consistent interpretations of breed standards anyway. Why, then, should we pretend that a standard, which as it now exists evokes a different imageistic interpretation in the mind of each individual breeder and judge, describes a single ideal type?

Canine breeds can and should be differentiated, bred and maintained on a dynamically balanced, heterozygous population basis without restriction to a closed, historic founder group. The closed studbook and the breed purity concept are, from a genetic point of view, simply unnecessary. Indeed, as we have seen, from the standpoint of maintaining a genetically healthy limited population, they are thoroughly counterproductive. Where is the logic in submitting each and every CKC breed to a registry system which guarantees ongoing, progressive genetic degeneration, loss of species vigour and hardiness, and saddles every breeder with the unwanted, unhappy responsibility of producing more and more unhealthy, flawed stock as time goes by? The notion that genetic disease can be controlled, much less eliminated, by screening programmes and selection has not been borne out by general experience. Those who promote such a notion are engaging in a cruel, self-serving deception. It may be that a breeder can sometimes improve his odds against producing defective stock in a given mating by screening the parents, but experience has proved that screening will not solve our genetic problems in any wider sense. Despite generation after generation of "clear" stock, bloodlines can still produce more and more affected animals. That is because our problems are inherent in the closed-studbook/incest-breeding system. In order to restore genetic health we shall have to adopt a different system.

It will be asked, "Just how will the opening of our studbooks to outcross stock bring about the elimination of genetic defects?" The answer is that it will not eliminate genetic defects. That need not be the end in view. If we could somehow eliminate all the various genes now known to produce harmful anomalies, plus all of those yet to be discovered, we would almost certainly find that the remaining genome was non-viable, that healthy reproduction and growth to maturity could not reliably take place. Genetic defects are not "eliminated" in nature. Instead, random mating and behaviour patterns that discourage inbreeding take care of the problem by ensuring high levels of heterozygosity and the consequent rarity of defective homozygotes. If we take steps to set up similar patterns in purebred dogs, we shall be able to reduce the level of expression of defective genes greatly, which is all that is required. The end in view is healthy stock, not "racial purity." Purged and purified bloodlines would be weak for other reasons, as has been explained. As the mapping of the canine genome progresses and RFLP, allozyme or microsatellite "markers" for common genetic defects are found, we shall probably then be able to use DNA studies to recommend matings that will avoid the production of defective homozygote

progeny -- provided that we have made enough genetic diversity available through outcrossing to give us the genetically distinct lines from which to choose! As things stand now, most breeds are so homozygous that it could prove extremely difficult to find matings which would avoid one genetic defect without reinforcing another!

New Structures for the Dog Fancy

VERY WELL, THEN, if we eliminate the closed studbook, how shall we decide what stock to admit for registration? One must begin, of course, with the existing body of registered stock. Thereafter, one way of proceeding might be to strengthen and empower the breed clubs. They should be granted responsibility and autonomy: responsibility for the welfare of their breeds, and autonomy to make the judgments and decisions necessary to fulfil that responsibility. It should also be ensured that the breed clubs are fully representative of all breeders, by making breed club membership a requirement for anyone to register stock he has bred or imported.

The first task of the breed clubs would then be for each of them to determine what sources of genetic inflow might best be employed in their breed. Breeders alone can command the collective expertise to make that decision and it ought to be theirs alone, but the designation of outcross sources should be obligatory, not optional. The Siberian Husky Club of Canada, for example, would have to decide where outcross animals might best be obtained for restoring heterozygosity to that breed; they might decide, for example, that dogs imported from Russia and perhaps even an occasional outstanding individual carefully selected from the present "alaskan husky" gene pool of racing sleddogs (which was derived largely from 1910-era Siberia imports that remained in Alaska) are two logical sources. Breeds which do not have their origins in autochthonous populations would have to seek outcrosses in similar related breeds, as Spaniels (English Springer) and Spaniels (Welsh Springer), or Retrievers (Labrador) and Retrievers (Flat-Coated). They would then have to set up inspection and test-breeding procedures for admitting outcross animals. Once the outcross sources had been designated, selection of candidate animals would in most cases be best left to individual breeders, who might then apply to the breed club for preliminary inspection of their outcross -- which ought not to be excessively rigorous. General soundness, reasonable temperament, proven working ability, approximate size and physique, and acceptable overall type would be adequate criteria, none of the foregoing to be rigidly interpreted. The outcross should then be registered provisionally by CKC, subject to breed club inspection of two generations of its progeny. The registry should remain permanently open to new outcross animals. It might prove desirable to set limits to the number of outcross dogs registered in any given year, proportionate to the overall breed population, in order that small populations not be swamped by excessive outcrossing. Some regulation of the process would obviously be necessary, but the best regulation would probably be breed club oversight and guidance of the process, backed up by CKC supervision.

Advantage should be taken of DNA analysis techniques by using them to monitor heterozygosity and relative kinship in major breeding lines. (It would also be a good idea for the Club to offer DNA profile parentage certification.) This technology already exists and is in use; it is rapidly becoming much more affordable. Limits should definitely be set on inbreeding, preferably by the breed clubs, but CKC should decide maximum allowable limits of inbreeding as a default setting. Only by the outright prohibition of excessive degrees of inbreeding will it be possible to make the transition to a balanced-heterozygote state for purebreds; otherwise old ways will continue through inertia and persistent typological thinking. Assortative mating can and should become the norm for the preservation of type, mating individuals which are phenotypically similar but unrelated or at least not closely related. The Club would have to monitor registrations, possibly performing occasional DNA spot-checks, to ensure that inbreeding does not take place; otherwise many would continue to breed from whatever dogs were in their own backyard rather than seeking breed club advice to find suitable individuals from unrelated lineage.

A Healthy Balance for Breed Identity

THE RESPONSIBILITIES of the breed club should not end with the designation of outcross sources and the inspection of outcross candidates. If the fulness of breed identity is to be achieved overall in each population, then the breed clubs should take on responsibility for balancing the various facets of that breed identity. Realistic, meaningful and workable systems should be introduced for monitoring temperament, for proving working ability and trainability, and for evaluating type and appearance. Championship shows would then become breed-club events, since the methods of evaluation and the various events required to test such qualities as temperament, vigour and endurance, working ability, and trainability would be breed-specific and under the breed clubs' oversight. That is not to say that a number of breed clubs might not band together to stage events for several breeds simultaneously at the same venue, but the all-breed show with all-rounder judges, under CKC rules for CKC Championship points, would eventually be history. To ensure wholehearted support and participation by breeders, it would probably be necessary for CKC to evolve some means of making clear on the papers of

every dog the extent to which that animal had been submitted to the testing and evaluation procedures of the breed club and with what result. Breed club input of information to the Club's database could be done by e-mail on the day of the event. Strong incentives for participation should be arranged and breed clubs should be so structured that they could not be autocratically ruled by individuals or cliques.

Registration certificates produced by CKC would carry much more detailed information under the new system than they now do. The computer power is now available to make this quite feasible. A certificate of registration should once again carry a pedigree of at least four generations. A two-tier certificate system would be necessary, as no dog would be eligible for breeding registered progeny until it had been inspected and evaluated by the breed club. Rating and measurement protocols are already being worked out by proponents of the Advanced Registry proposal. Broodstock certificates should carry a summary of the breed club's rating and evaluation of the animal, together with evidence of proof tests for temperament, working ability and trainability. All certificates should identify outcross lines and bear a quantitative estimate of the relative heterozygosity of the animal identified by the certificate.

Breed standards would require revision under the new system. The concept of disqualifications should probably be dropped in favour of a detailed rating system in which all breeding stock would participate. In the case of quantitative characteristics such as height and weight, a simple Bell-curve statistical description of the desired mean and range ought to be sufficient, without disallowing occasional extreme examples. Working abilities ought to be clearly defined in the breed standard and a basic performance standard given where possible. Clearer and more detailed descriptions of desired temperament and of qualities bearing on trainability ought to be part of the new standards. Prescriptive minutia should be minimal; it should be sufficient merely to describe the general distinguishing features of a breed, without an excess of cosmetic and conformation restrictions, except where indispensable breed points are involved. Type stringencies should be relaxed considerably, allowing most breeds to become moderately heterotypic; if qualities of working ability, hunting instincts and similar traits achieve greater emphasis, there will be correspondingly less need for extreme type requirements to distinguish breeds. Standards should be holistic descriptions of the breeds they identify, brief statements of essential breed qualities, rather than typological blueprints. It is imperative to subordinate typological thinking to considerations of utility, genetic health and hardiness. First a dog should be healthy, balanced, of sound mind in a sound body, able to fulfil his breed purpose; after that can come points of beauty and type but never again in the bizarrely exaggerated fashion that now prevails in the breed rings of championship shows.

It might eventually be found desirable to quietly merge scarce and consistently unpopular breeds, as well as closely similar breeds, with populations nearest to them in general characteristics, possibly initially designating them as breed varieties. Reasonable numbers are necessary for the maintenance of a healthy population. The number of breeds recognised has continued to grow, yet the total number of dog owners in the country may not have grown proportionally. A rare breed is not the same thing as an endangered species; breeds can come and go without damage to the canine species as a whole. Breeds known to be of low viability due to their dependence for breed identity on anomalies such as achondroplasia, may have to be dropped from the registry unless evidence is advanced that they can be upgraded to certain minimum standards of health and structural soundness.

Can it Really Work?

I CAN HEAR someone objecting, after having thought about the idea of a breeding and registry system in which outcross breeding was actually encouraged, "Surely this system will produce some dogs which are not even recognisable representatives of their breeds! What happens then?" Typological thinking dies hard. I used to worry lest my Siberian breeding programme should one day produce a dog or dogs whose ears were not fully erect. It never happened. Instead something much worse happened when I found that I was producing some dogs who ran a high risk of being unable to lead a healthy, normal canine existence, through endocrine malfunctions, immune system weakness, and the risk of blindness. To think I had worried about the possibility of a tipped ear, something which would not handicap or bother the dog in the least! Let me say the following, then, to those who worry that a balanced-heterozygote breed will engender "untypical" examples. It is far better that our breeding occasionally engender a dog deficient in breed type, than that we should consistently produce large numbers of dogs guaranteed to lead lives of suffering, creating anxiety, large veterinary bills, frustration and unhappiness for their owners. That is what we are doing now. Over sixty percent of Golden Retrievers, for example, will suffer from hip dysplasia, osteoarthritis or osteochondritis in their lifetimes. Is that to be preferred to the possibility of producing an occasional robust "mutt" lacking in breed type but who will nonetheless still make someone an excellent, happy, healthy companion? I am sure that it would take awhile for all of us to learn how to breed in this new and different way; I suppose we might produce occasional oddities in the process. Yet I am absolutely convinced that the good results we would quickly achieve would more than make up for the embarrassment of our failures. At the very least we should all have clean consciences once again, knowing that we were making our best efforts, using up-to-date genetic knowledge, to produce sane, healthy, robust canine companions. Let us not forget that as DNA mapping procedures

advance (there are at least two canine genome mapping projects now underway) our tools are going to improve and our ability to predict what our breedings may produce will be greatly enhanced.

As things now stand, the dog fancy is in a position which is frankly untenable. The CKC Board of Directors has unilaterally committed "reputable breeders" to the proposition of guaranteeing the "future genetic good health" of the dogs they sell. Yet those same breeders have no means of protecting themselves from the looming spectre of financial ruin should they be held to such a guarantee, otherwise to the loss of public credibility. Other than the continued elaboration of screening programmes and the Advanced Registry proposal, both of which are somewhat like applying an adhesive bandage to a severed artery, nothing is being done about making guarantees of genetic health a workable proposition. At present, purebred breeds -- all breeds -- show levels of genetic defects totally inconsistent with the practical maintenance of the Board's policy. Many honest, caring breeders are racked by torments of guilt and self-reproach brought on by the sufferings of defective dogs, yet it is really no fault of the breeders themselves! The fault, as has been demonstrated in this brief, lies with the closed studbook and the inbreeding system. If the consensus of the Club is truly that purchasers of purebred dogs have a right to expect genetically healthy animals, then the Board has no choice other than to do everything in its power to change the existing system so that healthy animals may once again be reliably produced! That will never happen just through Advanced Registries, higher Championship point requirements, more screening programmes, and Board policy pronouncements. The Club must take to heart the lessons of population genetics. It must open its studbooks to outcross stock on a permanent basis. It must take measures against the obsessive pursuit of breed type and the worship of breed purity, measures which will increase the health, utility, trainability and sanity of purebred dogs, measures which will balance the elements of breed identity. There are no credible "soft options" left.

One unfortunate reality which must be faced, however, in order to bring about any major changes involving the CKC will be the conservatism and resistance to change of the Board and of the "old hands" -- the ruling oligarchy of the Club. The CEO and the Board will almost certainly aggressively defend the status quo no matter how urgent the need for change. At present, for example, they turn down requests for the registration of new foundation animals with statements such as this one: "The CKC takes pride in registering dogs based on accurate and complete information and we will continue to strive for these high standards." Yet when that statement was written, the Club was still registering Canadian-bred litters whose parentage information was supported only by a signed registration application form filled out by the owners of the dam and sire. Under that system of information gathering it is regularly necessary for the Board to cancel litter registrations when it becomes evident that the parents of some litters are not both of the same breed. No one knows how many litters go unchallenged which, although purebred with both parents of the same breed, have their parentage misrepresented because the actual sire of the litter is not the dog entered on the application form. In the absence of DNA testing, how can the substitution of sires be detected?

Meanwhile the United Kennel Club, a "dissident registry" in Kalamazoo, MI, USA, which now registers about a quarter of a million dogs annually, has already instituted a process for the verification of parentage by DNA profiling! This is the first time that DNA profiling has been made routinely available to dog breeders, and UKC is the first canine registry in the world to offer such assurance of verified parentage. Innovations such as this make the Club's defensive statements about its high standards sound rather hollow.

nbsp; Anyway, those of us who seek reform will have to contend with a Club establishment which will attempt to make a virtue of the very things which most threaten the genetic health of CKC dog breeds: the closed studbook, the breed purity concept, the endless inbreeding, the constant refinement of type, the pre-eminence of the Championship show. Those who dare to challenge the existing system will have to put up with being made to look foolish or even villainous by the solemn pronouncements of the old guard. We should all realise that the Club establishment is unlikely to initiate serious action for change in the absence of grass-roots pressure from the general membership. It is up to us to initiate serious dialogue along the lines outlined in this brief, to research ways and means to promote a different, healthier method of purebred dog breeding, and to raise the consciousness both of novices and of old hands regarding the genetic dilemma which now faces us.

Deep structural change cannot occur without widespread debate among fanciers, because new and different concepts sound threatening when they are first described. Once the reasoning behind them has been adequately discussed, the threat often disappears. Someone may ask, for example, "What about these open-ended Breed Standards? A Bell-curve statistical description of a breed's height standard may be an adequate formula, but what if the mean is set at 22.5 inches and you don't disqualify the 25-inch dogs. Then maybe in a few years the mean may drift upward to around 24 inches, with hardly a single dog under 22 inches. What then?" My answer would be that the whole point of the balanced-heterozygote system is its healthy flexibility. A stubborn insistence on narrow tolerances in matters such as height at withers usually involves the sacrifice of other worthwhile qualities anyway, as too many otherwise good animals must be discarded only because they are a shade over standard. In the balanced system described, nothing at all need be lost. If the height mean of a 22.5-inch breed should drift upward to 24 inches, it would be because most of the breeders wanted a taller dog! Since the breed club would be advising breeders, measuring and rating dogs, maybe even suggesting matings, this sort of gradual change would occur only with the knowledge and acquiescence of the breed club, representing all active

breeders. Under a heterozygous plan with mainly assortative matings, nothing whatever is lost in such a gradual change. Should the height drift upwards and, later on, the breeders decide upon a return to the original mean, a simple shift in the emphasis of assortative mating will accomplish such a return easily, smoothly, with no genetic loss and no disturbance of other traits.

The whole idea of a dynamically balanced heterozygous breeding system is the retention of as much healthy genetic diversity as possible. Such diversity makes it easy for a breed to develop and progress in whatever direction its breeders wish. It also ensures that genetic problems are kept to a minimum no matter what changes of standard may occur. In the statically balanced homozygous system now in force, the more homozygosity increases with time and selective breeding, the harder it becomes for major change to occur naturally and easily, and the more pronounced genetic problems become. Once an allele has been "fixed" in homozygosity, no amount of selection can change that trait; only radical outcrossing can restore the lost alleles and such outcrosses will always upset the static balance completely, necessitating years of remedial inbreeding and selection, probably creating new genetic problems. I am convinced that a system based on a dynamic equilibrium of healthy dominant genes must inevitably be better than one which throws away most of the healthy genetic diversity in order to achieve static stability for homozygous recessive traits.

It is worth noting that the new system, if carried out at all conscientiously, would mean more work per dog for everyone. Breeders would necessarily invest more time and effort in their breeding stock in order for it to pass breed club requirements. This is by no means a negative factor. One ongoing problem in our society is that of large numbers of unwanted pets. Another related problem for the purebred fancy is substandard dogs produced by the non-serious "backyard" breeder and the puppy-mill profiteer. The suggested reform measures would discourage exploitative factions and reduce considerably the overall number of purebred dogs, while raising greatly the overall quality levels and ensuring that practically all purebred dogs were valuable, cherished, and wanted by their breeders and owners. The new system would greatly increase the inherent value of purebred canine stock. Purebred would then mean much more than just a paper certificate!

A Canine Revolution?

THE FOREGOING PRESCRIPTIONS may sound like a canine revolution. If so, the revolution would consist mainly of integrating many facets of the fancy which now exist in ghetto isolation, or of importing good ideas from other parts of the cynological world. In Europe, for example, many breed clubs have long held responsibilities for their breeds similar to those described above. The only really revolutionary features of this new vision of purebred dogdom are the permanently open studbook and the abandonment of incest breeding, and those represent simple, inevitable acquiescence to genetic reality. If there is one thing we can do which will be of lasting benefit to the dogs we breed, it is to endow each and every one with a healthy, heterozygous genetic outfit. If that is to become possible, the closed studbook must go and inbreeding must go. There are no effective alternatives.

These reforms would require considerable co-operative effort on the part of breeders, breed clubs and the CKC in order to bring them into being. A major part of the job would be to convince Agriculture Canada of the desirability and feasibility of these proposals, followed by amendment of the Animal Pedigree Act to facilitate them. Yet when we consider the threat to the very existence of purebred dogs posed by genetic disease, the economic loss caused by genetic defects, and their widespread unhappy effect on people's lives, can we deny that radical and decisive remedial action is required? The goals of a balanced-heterozygote breeding system producing healthy, hardy dogs and a balanced breed identity structure coordinating all the delightful activities of purebred dogdom, would be worth any amount of effort. Let us begin work now to bring those goals into existence! Future generations of breeders and fanciers will be grateful to us for so doing and what is more, we shall be doing the best and kindest thing for our very best friends -- our dogs.

Continue to read Part Four: Postscript, Bibliography, Glossary and Afterword

The Genetic Tide: Will it Leave Us High and Dry?

WE HEAR MORE AND MORE these days about genetic defects, with good reason. A year ago Time™ Magazine published a pre-Christmas exposé cover story on hereditary problems in purebred dogs. Now the Council of Europe urges EEC member states to adopt its "Multilateral Convention for the Protection of Pet Animals" banning the breeding of animals whose breed points handicap them, regulating breeders in an effort to halt the increase in inherited health problems.

Many breeds we used to think of as hardy natural types -- even tough Arctic animals like Samoyeds, Siberian Huskies and Alaskan Malamutes -- are now routinely screened for four or five different genetically-related problems. These include deep-seated, serious disorders: central nervous system problems such as epilepsy, immune system malfunctions such as autoimmune thyroiditis. In addition to hip dysplasia, we now worry about osteochondritis, elbow and patella dysplasia, half a dozen distinct eye problems, and more.

At first it was thought that x-rays, screening and selection would ensure genetic health for our dogs. But thirty years of hip x-rays have not wiped out HD, although progress has been made in some breeds.

Screening and selection for one defect is just fine. But what do you do when suddenly five or six distinct problems must be screened for? Veterinary costs soar. You must select *against* so many traits that your breeding programme is turned upside-down. Especially if you fancy a serious working breed, as I do: you cannot manage a four- to six-way screening schedule and still select for working ability, breed type and conformation. In a small kennel on limited funds, breeding only two litters a year, it just isn't practical.

The books on dog-breeding hold no answers. They tell us how to use inbreeding, line-breeding and outcrossing, they teach us the basics of Mendelian genetics; these help to manage one or two traits at a time. But genes don't assort one trait at a time! Genes are *linked* in groups on chromosomes. While we were all using inbreeding and line-breeding to "fix" desirable traits of breed type and conformation, something else happened, and now we get a steady increase in *unwanted* traits that we call genetic defects.

The science of "population genetics" is old stuff to wildlife biologists, but few dog breeders in this country know much about it. Yet it could have told us about the problems that we would have by practising artificial selection, breeding from small founder groups with no new gene inflow for decades, using sustained incest breeding without the brutal tempering influence of natural selection.

Today, when most registered breeds are fifty to a hundred years old, bred within a closed Studbook the entire time, population geneticists tell us that we cannot continue these practices any longer if we want healthy canine companions. They say new genetic inflow is needed to counter random drift in small breed populations and to restore heterozygosity -- genetic diversity -- where it has been lost through inbreeding. They tell us that we are overusing popular sires and add that the German Shepherd Dog, despite millions of actual individuals worldwide, has an effective genetic population of from 400 to 600 animals only! Time-honoured breeding practices are now labelled "genetic genocide".

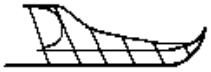
Breeds such as Salukis, Siberian Huskies, and Basenjis could easily restore hardiness and diversity by importing primitive stock from their countries of origin, but C.K.C.'s closed Studbook cannot accept such imports.

Perhaps the closed Studbook has outlived its usefulness. In the early days of purebred dogdom, it was a useful device to promote fixation of breed type. Now it has become a dead hand, dragging down the health of our beloved dogs.

The C.K.C., unlike most other Canadian livestock associations, makes no provision for grading-up, crossing, or new breed development. Its Studbook remains rigidly closed. Each C.K.C. breed is genetically isolated. No protocol exists for the acceptance of new foundation stock in C.K.C. breeds. The Club's procedures seem stuck in a nineteenth-century mould.

The upsurge in genetic problems -- and the media and government attention they attract -- make it obvious that radical change is needed. The question is, can it come in time? Or is our Club too inflexible to meet the challenge of placing real breed improvement above the demands of tradition and show-ring fashion? Is type more important than health? If we cannot breed healthy, hardy, happy dogs, there are those in our society who will question our right to breed at all.

-- This article was written just before the Seppala Siberian Sleddog became an evolving breed. It was published in "Dogs in Canada" magazine's February 1996 issue. Submitted by DIC to the Dog Writers Association of America annual competition, it won a Maxwell Medallion in the "Essays and Opinions" category for that year.



The Genetic Tide Continues to Swell:

Will DNA marker research stop the flood?

The tide of concern about genetic health continues to swell within the purebred dog fancy, driven on by scrutiny from without. The threat of punitive legislation, already a reality in Europe, is widespread in the USA and the contagion seems certain to reach Canada as well. Conventional screening methods appear to be a proven failure as far as curing genetic disease (rather than simply reducing it somewhat). As veterinarian breeder Ms. Chidiac-Storimans once wrote in *Dogs in Canada*, "obviously, breeding clear to clear does not work." Yet great optimism is expressed in canine journals despite the seeming crisis proportions of genetic disease.

DNA marker research now holds the limelight. The US$750,000 canine genome project at the University of Michigan, reported in the press in 1990 as expected to identify DNA marker sequences for over 400 canine genetic diseases, has actually established 625 markers and as a "demonstration project" was able to link one marker to a specific genetic disorder, copper toxicosis in Bedlington terriers. This and several other DNA tests for breed-specific disorders are now marketed by VetGen in Ann Arbor MI, where the University is also located. The Scottish Terrier Club of America recently paid US$50,000 to establish a DNA marker for canine von Willebrand's disease in their breed; other breed clubs are reportedly queueing up to pay similar sums for similar purposes. Obviously there is money to be made in canine genetic diseases, though perhaps not by dog breeders.

Even if every breed club had that kind of money to spend on marker development, and every breeder could afford $50 to $135 per test for all his dogs, there would remain plenty of room for doubt concerning whether the strategy of DNA marker tests followed by radical selection and culling would solve the problem of genetic disease. Gene pools of purebred dog breeds, already stripped and impoverished of genetic diversity by twenty or thirty generations of inbreeding and selection, may not withstand a massive wave of radical selection followed by yet more inbreeding. What happens when all or most individuals in a breed turn out to be "carriers" of the same defect? Breed gene pools represent only a fraction of the total canine species genome. Genetic diversity in purebreds is limited from the outset, by selection inherent in breed development and by the sometimes distressingly small numbers of founder animals when breed registries are first established. A gene pool is like a bank account - you cannot make withdrawals forever and never make a deposit. Yet the closed studbook system prohibits making more than one deposit! The fetish of "breed purity" demands that after the founder registrations the stud book must remain forever closed to new genetic input. When examined closely this concept of strict breed purity must be regarded as a racist ideal, similar in nature to the "scientific racism" promulgated by Hitler's Nazi party. Why do we denounce racism and eugenics on the human level, only to turn about and defend the selfsame ideals as the only decent norm for breeding dogs?

Any description or defense of a project involving breeding across existing breed lines for practical purposes, such as the Wirehaired Pointing Griffon Club of America project, is met with aggressive rebuke. If every effort to restore genetic health, hardiness, or working ability through outcross breeding is to be condemned as a betrayal of the "purity of the breed," then the entire purebred dog concept may be doomed to failure through inbreeding depression, the general loss of vitality and viability. Those who are quick to stigmatise serious outcross programmes as "Foufons" and "crossbreds" betray their utter ignorance of population genetics, yet that ignorance still meets with general approbation. Too bad, because at this point, the application of population genetics principles may be the sole strategy that can possibly pull the purebred dog fancy out of its genetic

dilemma.

Genetic diversity is held to be essential to maintain species soundness and environmental fitness, but genetic diversity is what most purebreds seriously lack. Responsible scientific opinion now connects this lack of diversity with the canine genetic crisis. However much the racist mind may condemn the idea, there is but one way to restore lost genetic diversity in a population, and that is by new gene inflow - in other words, by outcross breeding. When will the purebred dog fancy awake from its dream of purified bloodstreams and allow the new gene inflow necessary to restore genetic health to our dogs?

(This article by J. Jeffrey Bragg was a followup to the award-winning DOGS IN CANADA article "The Genetic Tide: Will it Leave us High and Dry?")