The concept of inbreeding generally provokes negative reactions amongst the public, due to the fact that incest is one of the strongest taboos in human society. There is a general conviction that incest amongst human beings causes almost immediately the development of serious genetic diseases.

On the other hand, in laboratories where experiments on mice are performed, there has been an effort to breed mice that carry a level of genetic similarity of almost 100%. The extreme level of homozygous genetics that is being researched has been achieved through over twenty generations of mice mating amongst siblings.

As cat breeders, we lie somewhere between these two extremes. Since the inbreeding we perform does not relate to humans we are not restrained by a taboo. Yet, our objective is not to create clones of the animals we work with. Our objective is to determine a pool of genes that we would like to preserve and create healthy offspring that possesses the sought after characteristics.

Conventionally breeders refer to the mating of related cats as “line-breeding” if the mating is seen positively and simply as “inbreeding” if the mating in question has a neutral or negative connotation. The term “incestuous breeding” is used in a context where there is an extremely negative connotation. From a technical perspective, all three terms have the same meaning, as they define the mating between animals who have common ancestors. For the purposes of this article, only the word “inbreeding,” intended in its purely technical meaning, will be used. There is no moral significance attached to the word in this article. The opposite of inbreeding is defined as “Outcrossing,” where two unrelated individuals are mated to produce progeny.

Whenever the name of a cat appears on the pedigree of both parents, there is a case of inbreeding. It is important to specify that we should not only consider five generations, as is usually done in pedigrees, but as many generations as possible. For Bengals it is possible to reconstruct a pedigree with eight to ten generations before reaching the earliest founding cats: Centerwall ALC, Rorschach F1, Tory of Delhi, and Finally Found. The ancestors of these founding cats are mostly unknown.

In the following paragraphs we will show how inbreeding leads to a steady decline of heterozygosis, a steady fixation of all genes (wanted and unwanted ones), and to an increase in genotypic similarity. Therefore, inbreeding increases the chances of offspring being affected by recessive alleles.

Every feature is defined by one gene, which is composed by two alleles, one coming from the mother and one from the father. For the feature chosen in Fig. 2, we will call the allele from the father X1, and the allele from the mother X2. In the generation of the grandparents there are four cats, each one marked by a different color: red, black, green and blue. In the generation of the parents the father will have an allele from each of his parents, so there are four possible combinations:

\[
\begin{align*}
X_1X_1 & \quad X_1X_2 & \quad X_2X_1 & \quad X_2X_2
\end{align*}
\]

The father will be one of these four combinations. For the mother, it will be the same thing:
Fig. 1: An example of a five generation pedigree: the sire's father and the dam's father is the same cat. This particular pedigree proves Spice Swiss Miss is the result of an inbreeding (half-sister/half-brother breeding).
Fig. 2: This picture helps to determine which alleles come from which ancestor. We are talking about any possible trait. For this reason we have labelled the two alleles with the letter X.

Fig. 3: This picture shows the different combinations for a half-sister half-brother breeding. The inbreeding coefficient is related to the probability that both copies of any given gene are derived from the same ancestor.
As can be seen in Fig. 2, by crossing the alleles of the parents we have sixty-four different possible combinations. Every combination is composed of an allele from the father’s side and an allele from the mother’s side. It is impossible to obtain a combination of two alleles from the same side. In the picture, this is demonstrated by the fact that none of the sixty-four possible combinations is composed by two alleles of the same color.

This is no longer the case if the cat is inbred—for example if his parents were half-sister and half-brother.

Figure 3 illustrates what happens (for example) with Spice Swiss Miss, whose pedigree we showed in Fig. 1. In the generation of the grandparents the same color figures twice: the two red couples of “X”s are the same cat (the grandfather—Spice Estragon). The parents are a half-sister and her half-brother, so they have one parent in common (X₁X₂).

There are eight possible combinations for the gene in question where the two alleles are identical, X₁X₁ or X₂X₂. These eight combinations are circled in Fig. 3. For these eight cases, the genes are homozygote by definition. The possibility of obtaining a homozygote gene is extended by 12.5%. Of course this is true for all the 20,285 putative genes on the cat’s genome. From this it follows that an inbred cat has an increased genotypic similarity—and this is exactly what we call the inbreeding coefficient of the cat in question (Fₓ).

If the common ancestor carries for a recessive allele (Fig. 4), the recessive alleles will pop out whether they are wanted (specific trait) or unwanted (a genetic disease). Four combinations out of the 64 will be homozygotes for the recessive allele, and 24 will be carriers of this allele. Consider, for instance, the gene for Progressive Retinal Atrophy (PRA), which causes progressive blindness. Carriers have normal vision, but statistically if one is mated to another carrier it is likely that one in four of the kittens will have PRA and go blind.

*“We must be careful not to ‘fix’ immunodeficiency when we are trying to ‘fix’ type.”*  
– Heather E. Lorimer

Different kinds of inbreeding will have different repercussions on the inbreeding coefficient. If we do a breeding it is important to calculate the exact inbreeding coefficient (F); between two cats which are already inbred, the inbreeding coefficient will be even higher. We have already seen that Spice Swiss Miss (Fig. 1) is the result of a half-sister half-brother.

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**Fig. 4:** This picture shows what happens if the common ancestor carries for an unwanted recessive allele (x₁).
breeding. If we take a closer look at her pedigree, we can see that Bridlewood A License To Thrill is also her Great-Great-Grandparent on the sire’s side and her Great-Grandparent on the dam’s side. When we calculate the exact coefficient of inbreeding, we have to take this matter in account and we get the following results:

<table>
<thead>
<tr>
<th>Spice Swiss Miss of 5 gen. 8 gen. 10 gen. Total</th>
<th>Babbling, F, 2014-09-12</th>
</tr>
</thead>
<tbody>
<tr>
<td>14,5% &gt;15,2% &gt;17,2% &gt;32,6%</td>
<td>12</td>
</tr>
</tbody>
</table>

If we study Spice Swiss Miss at 10 generations carefully, we will discover that some cats (particularly older ones) appear very often in her pedigree:

- Millwood Rajin Cajun: 35 times
- GC Nola Lamborghini of Joykatz: 30 times
- Gogees Roar O Raja of Belltown: 26 times
- QGC Gogees Dynamo Glow of Bluebloods: 20 times
- Millwood Trademark: 19 times
- Gogees Kimba Lee: 19 times
- Snowbear Cloud Nine of Hugable: 19 times
- Jeweliard Marilyn of Joykatz: 18 times
- Millwood Cajun Queen of Gogees: 17 times
- Millwood Rave Review: 16 times
- Gogees Nitro Glistening: 16 times
- Millwood Pennybank: 15 times

At the beginning of the twentieth century biologist Sewall Wright created a mathematical formula to calculate the exact inbreeding coefficient (F) (Fig. 5).

\[ F_X = \sum \left[ \left( \frac{1}{2} \right)^{n_1 + n_2 + 1} \right] \]

\[ 1 + F_A \]

This formula can be easily inserted into a pedigree program, so that the inbreeding coefficient can be determined by anyone. For instance, pawpeds.com offers this service. It is evident that such a program is only accurate if it contains thousands of pedigrees in its database.

We have determined the inbreeding coefficient of a dozens of cats and have found out that the **average inbreeding coefficient in the Bengal breed is between 25 and 35%** (Fig.6).

**How much inbreeding is too much?**

In scientific literature, much has been written about the negative side effects of excessive inbreeding, which are referred to as inbreeding depression. Robinson lists the following phenomena as resulting from inbreeding depression:

- Decline in birth weight (small, thin and lethargic kittens)
- Development problems (below standard individuals)
- Smaller average litter size
- Increase of the number of stillborn or abnormal kittens in litters
- Problems in reproductive performance (in both sexes)
- Weaker immune system (more illness at any stage of development)
- Physical indications (asymmetry, crooked noses, uneven eye size, etc.)
- Regular appearance of cancer in young cats.

In general, it is impossible to predict what form inbreeding depression might take and when these phenomena will start to show. There are very few recommendations for cat breeders. According to population geneticists, the average coefficient, of all the matings we do in a breed, should increase by less than 0,25-0,5 percentage points per generation. If the increase is higher, the population will be at risk of health problems due to inbreeding.³ In a leading German cat magazine⁴ there has been a recommendation to never exceed an inbreeding coefficient of 15%.

Compared to dog breeders, the level of inbreeding accepted by cat-breeders is extremely high. The Fédération Cynologique Internationale (FCI) recommendation for rare breeds is that the inbreeding coefficient should never exceed 10%. In England, the Kennel Club publishes every year the average of the inbreeding coefficient for all dogs registered in a

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**Fig. 5:** Sewall Wright: Coefficients of Inbreeding and Relationship. In: The American Naturalist. Volume 56, 1922, p. 330–338
Fig. 6: The list above shows the inbreeding coefficient of some of the cats analyzed. Wherever the coefficient is indicated as greater than (>), it means that the pedigree is incomplete for the amount of generations considered. In this case, every unknown cat is considered a complete outcross by the program, even though he is probably not.

certain breed during the past year. Examples of some popular breeds are shown in Fig. 7.

A study of Standard Poodles discovered that dogs with a coefficient of inbreeding of less than 6.25% lived on average four years longer than those with coefficients of inbreeding of over 25%.⁵

A study of Leonbergers could prove that there is a significant difference in the number of live-born puppies when comparing litters with coefficients of inbreeding over 10% and litters with a COI lower than 10%.⁶

Interesting studies on inbreeding have been done on farm animals, such as cows, sheep, and hens, since there is an interest in understanding how inbreeding affects the profitability of the farming industry. For example, for hens, the more the inbreeding coefficient is raised, the less eggs will be produced per year. The
Agricultural Business Research Institute claims that inbreeding depression is likely to be more apparent once inbreeding levels increase to over 10%. As a very rough guide, there is often a 2-20% decrease in performance of the trait per 10% of inbreeding coefficient.

A new long-term goal for the Bengal breed?

If we consider that the inbreeding coefficient in Bengals is about ten times higher than the one in German Shepherds, if we realize that all the animals who live in the farms have a lower coefficient of inbreeding, maybe we should start worrying. It is not where we are today that is the main problem—most Bengals are still healthy—it is the direction of our breeding that is the problem. If we continue this way, we know from other breeds (of cats and dogs) that problems will appear in the future. In the best interest of the Bengals we should set a new long-term goal for our breed: not to exceed an inbreeding coefficient of 15%.

This brings to mind two crucial questions about breeding.

Question one: Why is the inbreeding coefficient in Bengals currently so high?

The answer can be found in the early pedigrees of the Bengal breed. Jean Mill started the Bengal breed with very few cats, and all of today’s Bengals are somehow related to the earliest founding cats: Centerwall ALC, Rorschach F1, Tory of Delhi, and Finally Found. As soon as Jean Mill had two producing F3 males (two full brothers: Millwood Destiny and Millwood Trademark), she bred these studs back to the mother (Millwood Praline F2) and to the sisters (Millwood Polysport F3 and Millwood Rosetta Stone F3). This was the beginning of the Bengal breed and the source of our long-term inbreeding problem. In 1986 and 1987 Jean Mill registered the litters shown in Fig. 8, which had an already very high coefficient of inbreeding (COI).
If we calculate the inbreeding coefficient of one of our cats nowadays, and we manage to go back eight or ten generations, these very first close inbreedings are always taken into account.

Later, a few very successful males such as OS CH Millwood Italian Filigree, Nairobi’s Jungle Jaguar, RW QGC Dicaprio of Starbengal, IW SGC Hunterdonhall Tarzan, IW OS SGC Bridlewood A Licence To Thrill and, last but not least, RW OS SGC Stonehenge Wurththawate of Snopride had a tremendous impact on the breed because they were used for dozens of stud services and have each produced at least forty-six breeding kittens. It’s because of these studs that the Bengal breed could evolve at such a tremendous speed. They gave us the rosettes (Jungle Jaguar and Dicaprio), the contrast (Thriller), and the wild look (Tarzan and Wurthy) that are so appreciated in today’s show halls. However, did they only pass on their good traits? Probably not. Some of these cats probably carry for HCM, PRA, FCK, PK Def. etc., and that may be passed on to their descendants as well.

For these two reasons it is nowadays almost impossible to find two Bengals unrelated to each other. This is alarming, especially in a breed known to have genetic health problems (HCM, PRA, PK Def., etc.).

**Question Two: How can we decrease the current level of inbreeding in Bengals?**

First of all, we should avoid further inbreeding, and focus more on selective breeding, even if this means progressing more slowly, and perhaps winning less at shows. Secondly, we should encourage the sharing of our lines, particularly if these lines are not very spread out yet. One single stud should never again breed too many queens—this can happen on a voluntary base or be imposed by an association such as TICA. Some breed clubs of the dog fancy such as the German Club for Leonberger dogs, already have restrictions on the use of stud dogs in their Breeding Regulations. Thus, a male is not allowed to sire more than seven litters per calendar year.¹

The time has come to strengthen our gene pool through outcrossing, to maximize genetic variability in the cats we produce, to insure hybrid vigor, and to maintain a healthy gene pool for the long-term survival of the breed. This project requires the input and co-operation of a large number of breeders, not only a small minority. It takes a conscious effort and agreement within a breed to value health and actively breed toward this goal.

We should also continue to work with ALCs because it is an effective way to introduce new (unrelated) blood. Of course, as in the first days, it would be wise to breed the ALCs to Domestic Shorthairs or queens of other breeds—this would be the best way to start all over again.

As a more radical solution, we should consider outcrossing our SBTs to other breeds (Ocicats or Egyptian Maus) or using non-pedigreed cats in our programs. Nowadays we could carefully select these cats and test them for as many recessive genes as possible. This would allow us to increase the genetic pool without introducing unwanted alleles such as long hair, diluted color, non-agouti, or many genetic diseases. After World War II Russian Blue-breeders enlarged their genetic pool by breeding to British Shorthairs, Oriental Shorthairs, and Siamese. Should we follow the tracks of our fellow cat breeders?

From a legal point of view, the offspring between a Bengal with a non-pedigreed cat can be registered in TICA as an A0N. As soon as this non-permissible outcross is four generation away, the kittens get a SBT registration and can compete in a show. This is exactly how some breeders introduced the silver color into the Bengal breed: they did an outcross with a silver American Shorthair and four generations later, they had SBT silver Bengals.

As a more general provision, TICA, as the world’s largest genetic cat registry, could take a step forward and add software to calculate the inbreeding coefficient in the software that creates the pedigrees. I am convinced that many breeders are not aware of the dangers we are taking because they have never calculated the inbreeding coefficients of their breeding cats. Probably things would change quickly if the inbreeding coefficient was marked on all the registration documents and on the printed pedigree.

Bengal breeders need to know the “old lines” to see how they are so inter-related. The better educated and knowledgeable they are, the better chance they have to make good and intelligent breeding decisions. For this reason, [bengalpedigrees.com](http://bengalpedigrees.com), the largest pedigree database for our breed with over 17,000 pedigrees, will hopefully soon add on their homepage a user-friendly tool that allows us to calculate the exact coefficient of inbreeding. The [pawpeds.com](http://pawpeds.com) database works fine but only contains the pedigrees of a little over 8,200 Bengals.
Picture this: You are selling or buying a breeder cat to/from a friend (or the two of you are trading cats). You trust her and you are sure she will do what's right in every respect, so the two of you don’t use a contract. All goes well initially, and then you start discovering that the two of you have different expectations and understanding opinions about what should be done in any of a hundred aspects...and end up going for each other’s throat. Goodbye, friend!

As the individual in TIBCS who is responsible for handling ethics for the Executive Board, I have seen a lot of ethics complaints, but the ones that are hardest to resolve are the ones where breeders are on both sides. Bad feelings, and the resulting complaints, have resulted from such (relatively unimportant) matters as one party not providing the cat’s registration in what the other party believes to be a timely manner to disputes over whether the buyer can use the seller’s photos of the cat!

Agreements between breeders don’t have to be complex, though as the Code of Ethics requires, they must be in writing and signed by all parties (COE, Section 8). Think of it as a way of managing the expectations you and your counterpart have about the handling of your cat and the business end of your deal.

Besides the financial details (how much the cat costs, when the payment(s) will be received, and whether the deposit is refundable, who pays for shipping) you should list what the seller will do and what the buyer will do IF certain things arise, especially these three things:

1. What will each of you do if the cat isn’t fertile? Include in the description what constitutes infertility—breeding with a proven mate for two years? Having only two viable kittens at the end of a year and a half? Having closed pyometra and necessitating spaying? What must the buyer do—have the cat ultrasounded? Have the cat given a course of antibiotics in case of infection? What will the seller do—replace the cat, and if so, when?

2. What will each of you do if the cat dies? Does the buyer need to have a vet look at the body to ascertain the cause of death? Will the seller replace the cat, and with what type of replacement?

3. What will each of you do if the cat is later diagnosed with a disease or genetic condition, such as Feline Leukemia? PRA? HCM?

Make sure the agreement mentions everything that you (whether you are the buyer or seller) feel is important. If you are a buyer and the initial condition of the cat is of great importance, state what will happen if the cat arrives with parasites. If you expect the cat or its parents to have been tested, state which tests, the date that you will receive the test results (if possible), and what will be done if the cat(s) fails the tests.

If you have a sample contract that you think might be useful to others who are designing or updating their contracts, or that has wording in it that others might like to paraphrase in their contracts, send it to webmaster@tibcs.com, and she will add it to the website.