Genetic Characteristic of the Usual Form of the Polydactyl Gene in Cats: Especially Maine Coon Cats

By Janet Marr

It is the intent of this article to describe, compare and contrast the usual form of the trait for polydactyly in cats especially in Maine Coon Cats. The usual form of polydactyly will be defined as the trait commonly seen in Maine Coon Cat especially those familiar to organizations such as Mcpolys (http://www.mcpolys.com) This discussion will show that the usual gene for polydactyly is harmless even when homozygous. There is no sex link and there is complete penetration of the gene. This article will illustrate by making comparisons to other traits, that there is a high probability that there is more than one gene for polydactyly in cats. To demonstrate this there will be comparisons made to other cat breeds such as the Cornish Rex and Devon Rex. Comparisons will be made to the Manx and Scottish Fold Breeds in order to illustrate that the usual gene for polydactyly is harmless. There will also be an overview of the Danforth Study in which polydactyl cats were actually bred and studied. A brief reference will be made to the German Law, which intends to ban the breeding of polydactyl cats. This ruling maybe based on misrepresentation or incorrect translation of the Danforth study. The split toe trait in cats will be referenced in order to show that this condition is not related to the poly gene. The historical importance of this trait will be documented for polydactyl in the Maine Coon breed of cats. The use of the terms pre-axial and post axial will be defined and their importance will be discussed. It is hope that by understand this trait the reader will see that the usual trait for polydactyly in cats is harmless and needs to have it’s rightful place on the show bench.

Simple Inheritance in breeding a poly to a non-poly

Currently the gene for extra toes in cats is represented by the symbol “Pd”. The capital “P” represents the dominant gene for extra toes and the lower case “d” represents the recessive standard toe configuration of 5 toes on front paws and 4 toes on each back paw. Since this trait is not sex linked no reference need be made to the origin of the gamete. The gamete is produced from the union of two mature reproductive cells, an ovum (from female) or a sperm (from male), that unite to produce a zygote. A zygote is the newly formed fetus or kitten from the union of the two gametes. So in the below chart you see the union of a heterozygous polydactyl cat “Pd” bred to a standard footed cat “dd”. It should be remembered that a heterozygous polydactyl had one parent that was a poly “Pd” and one parent who had standard toe configuration “dd”. The recessive form “dd” of the toe configuration will be referred to as the standard toe configuration because all the major breed associations use the 5 toes in front and 4 toes in back as the standard.

<table>
<thead>
<tr>
<th>Gametes from normal footed cat “dd”</th>
<th>P</th>
<th>d</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d</td>
<td>Pd</td>
</tr>
<tr>
<td></td>
<td>d</td>
<td>Pd</td>
</tr>
</tbody>
</table>

Gametes from Polydactyly “Pd”

In the above checkerboard diagram the mating of a heterozygous poly cat to a standard footed cat will produce the following. This assumes that the litter has 4 kittens. Two of the off spring will be polys and two will be standard footed. The kittens produced in the first two quadrants will be capital “P” and lower case “d” so they will be polys. The kittens produced in the second two quadrants will be recessive “dd” so they will be standard footed kittens. This is the reason that the DNA markers for polydactyly will be the same for all the poly kittens and the DNA marker for the standard footed kittens
will be the same in each litter and for each family of related poly cats. However, all the poly kittens will be different from the non-poly kittens. By doing a DNA sample on the poly kittens and non-poly kittens in the same litter it should be possible to find the DNA marker for polydactyly. By comparing several generations of related poly and non-poly cats the difference in the dominant and recessive genes for the number of toes in cats should be apparent. These are the assumptions that are being made for the DNA study being conducted at the University of California by Dr Leslie Lyons.

**Poly to Poly Breedings**

When you breed a poly to a poly you introduce new variables. First you must know if you are breeding a heterozygosis poly or a homozygous poly. Let’s consider the case of heterozygosis poly breeding. This means the parents in the mating came from parents of a poly to a non poly mating. The symbol for each parent will be “Pd”.

| Gametes from Polydactyly “Pd” |  
|--------------------------------|--------------------------|
| P                             | d                        |
| P                             | PP                       |
| P                             | Pd                       |
| d                             | d                        |

In the above checkerboard mating if there were 4 kittens produced then theoretically there would be one homozygous poly “PP”, two heterozygosis polys “Pd”, and one standard footed kitten “dd”. In this proposed mating it is assumed that the poly gene is the same gene. If the poly gene coming from one parent were different than the poly gene coming from the other parent then there would not be a homozygous poly. This would be like breeding a Cornish Rex to a Devon Rex.

**What If There Are Different Forms of the Poly Gene**

Even thought the Rex genes for the Cornish Rex and the Devon Rex are recessive, their genes are different but have a similar effect (curly coat). The Cornish Rex gene is symbolized by “r” and the Devon Rex gene is symbolized by “re”. So if you breed a heterozygosis Cornish to a heterozygosis Devon you will get kittens with normal hair. If you breed a homozygous Cornish Rex “rr” to a homozygous Devon Rex “re re”, then all the kittens will in theory have coats coming from each breed. The Cornish Rex gene was discovered first and was formerly known as “rex-1” and the Devon Rex gene was know as “rex-2”. To make a point the old nomenclature will be used in the following theoretical mating.

| Homozygous Gametes from Cornish Rex “rex-1” |  
|--------------------------------------------|--------------------------|
|                                           | rex-1  | rex-2  | rex-1  | rex-2  |
| Homozygous Gametes from Devon Rex “rex-2”  | rex-2  | rex-1  | rex-2  |  
|                                            | rex-2  | rex-1  | rex-2  |  

All kittens will have the two different genes for curly coats in cats.

This can be useful when trying to explain what would happen if we have a second Polydactyl “P” gene. This could be symbolized as “P-1” and “P-2”. So if we bred a heterozygosis poly to another unrelated heterozygosis poly we can not assume that both poly genes are the same. In this case the following mating would produce this theoretical litter of kittens.
So if there were 4 kittens produced in this litter the kitten from the first quadrant would have extra toes that were coming from the genes “P-1” and “P-2”. This is what could explain cats found in the wild cat population with 9 toes or more on the front feet and 8 toes or more on the back legs. The kittens coming from the theoretical combination of the second quadrant and third quadrant would be a poly with no more than 2 extra toes per foot. The kitten from the fourth quadrant would have standard feet. This is why organizations such as Mcpolys at http://www.mcpolys.com recommend that breeders only bred a poly to a non-poly. In this way you can get some poly kittens and some standard footed kittens. The standard footed kitten can be show. Due to their heavy boning because of their poly heritage, they can do well on the show bench.

Other Dominant Genes, Manx

A dominant gene that causes serious health issues, is the Manx gene or the tail shortening gene. As reported by Robinson, 2nd edition, (1977) “It has been know for some time that Manx taillessness is inherited as a dominant trait, with the symbol “M” This has been confirmed and, what is more important, the accumulation of breeding data makes it highly probable, if not certain, that individuals homozygous for the Manx gene die prior to birth. The evidence for this is (1) an apparent absence of pure-breeding strains of Manx and (2) a decrease of the average number of young per litter for mating of Manx to Manx. The reduction is from an average of about four to three living offspring per litter.” ...Also noted was a reference to Todd, 1964, Howell and Siegel, (1966) that “a number of visceral organs also seem to be affected in one way and another.” Below is an illustration of what happens in a Manx to Manx breeding. Note that it is believed that all “MM” kittens die in utero or before birth.

Gametes from Manx “Mm”

<table>
<thead>
<tr>
<th>Gametes from Manx “Mm”</th>
<th>M</th>
<th>m</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>MM (dies in utero)</td>
<td>Mm</td>
</tr>
<tr>
<td>m</td>
<td>Mm</td>
<td>mm</td>
</tr>
</tbody>
</table>

Robinson continues “ thus, the Manx seems to be lethal when homozygous and apparently, semi-lethal at all times. One aspect of this is a preponderance of females among the viable Manx offspring, as if the males are less likely to survive. Also, examination of Manx still-born kittens, and those which died before the age of twelve months, revealed a greater number of both skeleton and organ anomalies than was shown by those Manx cats which lived beyond the twelve months.”

Rumpy to a Stumpy Breeding

The Manx standard according to the CFA Show Standard for April 30, 2005 to April 30, 2006 calls for the following:

“TAILLESSNESS: appearing to be absolute in the perfect specimen. A rise of bone at the end of the spine is allowed and should not be penalized unless it is such that it stops the judge’s hand, thereby spoiling the tailless appearance of the cat. The rump is extremely broad and round.”
According to the 3rd Edition of Robinson’s (1997, pg 204) *Genetics for Cat Breeders*, “the absence of a tail is readily apparent although careful examination has shown that the loss can be relative. In all four types of Manx taillessness have been distinguished. The true Manx is known as “rumpy”, in which no tail vertebrae can be observed... A second type is “rumpy riser”, in which an extremely small number of tail vertebrae can either be seen or felt as an upright projection usually immovable. The third type is “stumpy”. Here, the tail is longer and usually moveable although often deformed, knobby and kinked. The forth type is the “longie” and possibly is the rarest of the four. The tail is longer than many of the above (though shorter than normal) and is of more normal appearance.” It has been traditional for a Manx breeder to breed a “rumpy” to a “stumpy” in order to lessen the number of birth defects. It is ironic that in the CFA standard for the Manx a disqualifying trait is “incorrect number of toes”. Robinson continues with many more descriptions of spinal damage and spinal bifida (open spines). (Robinson, 1997) “It is well known that the homozygous Manx is a prenatal lethal condition but it is only comparatively recently that the moribund fetuses have been identified. These have been detected at as early as five weeks gestation as abnormally small and globoid fetuses with gross malformations of the central nervous system (Basrun and DeForest, 1979).” It should be noted that 4 forms of the Manx are heterozygous, “Mm”. So even when a breeding is done with a rumpy to a stumpy, it is still breeding a dominant “M” to a dominant “M”. Therefore, 25% of all kittens will be “MM” and thus born dead or reabsorbed prior to birth.

**Danforth Study**

This is in contrast to the Danforth, 1947, *(Heredity of Polydactyl in the Cat)*, in which “Skeletal, muscular, nervous and vascular systems all show modification in the polydactylous feet but except for the limbs no constant deviations from normal have been reported for the extra toed animals. For this study two extra toed female cats were bred to nonpolys in a control laboratory setting. The offspring were then mated in various combinations. According to the study “the breedings produced 234 normal and polydactyl kittens in 55 litters bred in the course of the study.”... “Since in the guinea pig one form of polydactyly is lethal when homozygous the possibility that polydactylly in the cat is also lethal naturally suggest itself, but the following considerations lend no support to such assumption. If we were indeed dealing with a gene, which is lethal when homozygous, its effect should appear only in litters from “PXP” matings. In the 31 litters (“PXp” and “pXp”) in which there can be no question of homozygosis of “P”, the 135 kittens averaged 4.35 to a litter. If this value is taken as an approximate norm and it is assumed that all individuals homozygous for “P” are eliminated before birth, the average size of a “PXP” litter should be about 3.26 instead of the 4.12 that were actually found. Further, if “P” were lethal when homozygous, only two-thirds instead of three-quarters of the young actually born should be polydactyl giving an expectation of 66:33 instead of the observed 77:22. Thus these data lend no support to the assumption that polydactyly in the cat is lethal when homozygous.” Unlike the Manx, “Of 100 consecutive polydactyl kittens whose sex was checked at birth, 52 were recorded as males and 48 females. While the data presented are not extensive enough to warrant elaborate statistical treatment, they are sufficient to show that the type of polydactyly studied behaves as a simple dominant with good penetrance, but variable expression, and to indicate that there is no reason to suspect the gene of being lethal when homozygous.”

**German Ban**

The ruling by the German government to ban the breeding of polydactyl cats may not be based on actual fact. Could this be a misrepresentation of the Danforth study or just a simple problem with translating the article from English to German? According to King, 2005 “In their infinite wisdom the German Federal Government ascertained that polydactyl was a semi-lethal defect and therefore placed a breeding ban on them. A paper by S and H Willer provided the main evidence in the
Expertise for the TierScg. They quote that polydactyly is an “autosomal dominant semi-lethal error with modification effect.” This quote is referenced by a piece of work by C. Danforth, 1947, “Heredity of Polydactyly in the Cat.” However, nowhere in Danforth’s research does he suggest that Pd gene (the gene responsible for polydactyl is a defect or harmful in any way. To the contrary Danforth actually sums up his research paper “The trait is not related to sex, and no evidence is found that its gene is lethal,” Furthermore, responsible polydactyl breeders will only ever work with the “Pd” gene and will only ever do a poly X non-poly mating, yet Danforth’s research actually found no problems with homozygous polydactyl and therefore, poly X poly matings.” Could the German ban actually have been started because the writers of the ban did not understand Danforth’s work?

Scottish Fold

Another dominant gene causes the folded ears in the Scottish Fold. According to the Fourth Edition of Robinson’s Genetics for Cat Breeders & Veterinarians (1999, pg 180) “the fold is produced by a dominant allele “Fd” with incomplete penetrance. Unfortunately for the popularity of the breed, the cartilage defect is echoed throughout the skeletal system, but appears to cause no other symptoms for the majority of heterozygotes “Fd”. However, the homozygote “FF” may have a crippling overgrowth of the cartilage of the bones know as osteodystrophy. The bones of the tail become palpably thickened and stiffened, and the bones of the legs become thickened and arthritic, especially around the feet. Normal bone growth is disturbed because of abnormalities of the epiphyseal plates. Ossification is also deficient and irregular. Eventually in these cats, they lose the ability to walk properly and suffer considerable discomfort.” As shown in the below checkerboard chart 25% of the kittens would be “FF” and thus suffering from problems with walking. This diagram illustrates the breeding of a Folded Eared Fold to another Folded Eared Scottish Fold.

<table>
<thead>
<tr>
<th>Gametes from Scottish Fold “Fd” “fd” (heterozygote)</th>
<th>Fd</th>
<th>Fd Fd</th>
<th>Fd fd</th>
</tr>
</thead>
<tbody>
<tr>
<td>(heterozygote)</td>
<td>Fd</td>
<td>Fd</td>
<td>fd</td>
</tr>
<tr>
<td></td>
<td>fd</td>
<td>Fd fd</td>
<td>fd fd</td>
</tr>
</tbody>
</table>

The editors of 4th edition of Robinson (pg 180) continues to note that “To avoid the breeding of the homozygote, “Fd X Fd”, the Scottish Fold cat should only be mated to other breeds (British Shorthairs have been used for this purpose) or normal-eared cats which have been bred from Scottish Folds. The problem with the latter approach is that because this gene is an incomplete dominant, some Folds with the mutant allele have normal appearing ears. It is disturbing that even in the most careful breeding program, a small proportion of the cats produced develop the crippling form of the abnormality. Very rarely heterozygote “Fd X fd” cats also suffer from the abnormality.” The fact that the trait is incomplete dominant is the problem since without a DNA test prior to breeding it would be impossible to know if the cat was an “Fd X Fd” or an “Fd X fd”. This difference seems small but it could mean the difference between crippled or normal kittens. Yet in the Fourth Edition of Robinson, the folded ear trait is listed as a “cosmetic” trait and polydactyly is called “impairing”.

It should be noted that none of the 234 polydactyl kittens in the Danforth Study had any problems related to being born polydactyl or from having polydactyl parents. Kittens did not die in utero. Kittens were free of most birth defects. Out of the 234 kittens there were two that developed hernias and one with some degree of ataxia. This is in sharp contrast to the Manx kittens that died in utero or were born with gross birth defects. The Scottish Fold kittens were born free of birth defects but later developed crippling conditions. Yet both these breeds are accepted with full show status in most cat
associations. The dominant gene for polydactyl should be grouped with other harmless dominant genes such as the Selkirk Rex, American Wirehair or American Curl.

**Split Toe**
There is a condition known as split foot that has been incorrectly associated with polydactyl. The split foot or sometimes known as lobster foot is not a form of polydactyl. It is abnormality caused by the gene “Sp” (according to The Book of The Cat, 1980, pg 42) and “Sh” (according to Robinson, 1997, pg 212). The gene has nothing to do with the gene “Pd” for Polydactyl.

Historical Significance of Polydactyly for the Maine Coon Cat

In several early publications about Maine Coon Cats there are notations that many of these cats were polydactyl. The below sketch was published by the Maine Coon Breeders and Fanciers Scratch Sheet in the Spring Issue of 1970. The issue makes note that “our MCBFA Polydactyl Standard has been voted in by our membership, and the wording is as follows: “The Maine Coon Polydactyl Cat should conform to the Standard of the Maine Coon, with the exception that multiple toes are allowed on either fore or hind paws, or both.” For more information on this see the article on Historical Reference to Polydactyl in MCBFA published in the Scratch Sheet (Marr, Spring 1999, http://www.furkats.net/mcbfa.htm). It is clear from this sketch that the intent of MCBFA was the standard was to be written for the polys with extra dew claws.
Pre-Axial vs. Post-Axial

This brings us to the issue of pre-axial vs. post-axial. According to Solveig Pflueger, MD, PhD, FACMG (Cat Fanciers’ Journal, 1998, pg 5) “polydactyly in mammals is classified by embryologists as either pre-axial or post axial. Axial refers to the folding of the embryonic limb. The thumb side is before the axis, or pre-axial, while the little finger is considered post-axial. When polydactyly is seen in the human, it is usually post-axial. In other words there is an extra little finger. Most polydactyl cats, on the other hand, have a form of pre-axial polydactyly with the extra digit(s) on the thumb side of the foot instead. The usual form of feline polydactyly results of a simple autosomal dominant trait. It does not appear to affect the cat adversely, some owners may argue that the big feet of the polydactyl enable the cat to walk better on the surface of snow, a snowshoe effect, and thus, may enhance survival in New England winter, there is not real evidence
that polydactyly has any significant natural selective advantage or disadvantage, however, there may be an element of artificial selection based on people’s preference that has served to maintain the polydactyly trait in domestic cat population.”

In the Marilis Hornidge (1981, pg 39) book called, That Yankee Cat, the Maine Coon, she makes note that “the number of claws in those paws perhaps the most controversial of all issues in the final stage of setting up a standard. The traditional Maine Coon was frequently a polydactyl or a many toed cat, a genetic mutation, which occurs with greater frequency in the upper north east of the United States. In the greater Boston area, for example, almost twelve percent of the feline population shows this trait, which to some people is endearing but to others is a deformity. Whatever the reason for its abundance in this geographic area the “poly” or snowshoe-footed cat is part of the legendary Maine Coon. They were so dear to the hearts of the originals group of enthusiasts who drew up the MCBFA Standard that, rather than divide the ranks, a special classification with its own standard was set up for them. This was the last variation on the standard to fall victim to the striving for a single standard to be adopted fancy-wide. Some breeders who love them still keep and breed a few as specialty kittens, although they cannot be shown, and the practice is frowned on as pure indulgence by their colleagues and competitors.”

In summary the usual gene for polydactyly in cats is harmless. The usual form has extra digits on the inside of the front legs as extra dew claws. The trait is inherited as a simple dominant gene with no sex link. Since there could be more than one form of the gene it is recommended that a polydactyl be bred to a non-poly. There are no supporting data to indicate that the gene for polydactyl is lethal even when homozygous. The German government may have banned the breeding of polys because of a translation error in exiting research. This trait has historical significance for the Maine Coon Cat breed. There are many Maine Coon Breeders and Fanciers who would like to see this trait preserved and accepted for full show status.

Bibliography


Danforth, C. H. Heredity of Polydactyly in the Cat Department of Anatomy Stanford University School of Medicine, J Hered, 1947: 38: 107-112.


Maine Coon Breeders & Fanciers Association (MCBFA), The Scratch Sheet, Spring, 1970.


Pflueger, Solveig, MD, PhD, FACMG “Polydactyly and Related Traits”, Cat Fancier’s Journal, Fall, 1998: 5-6.

