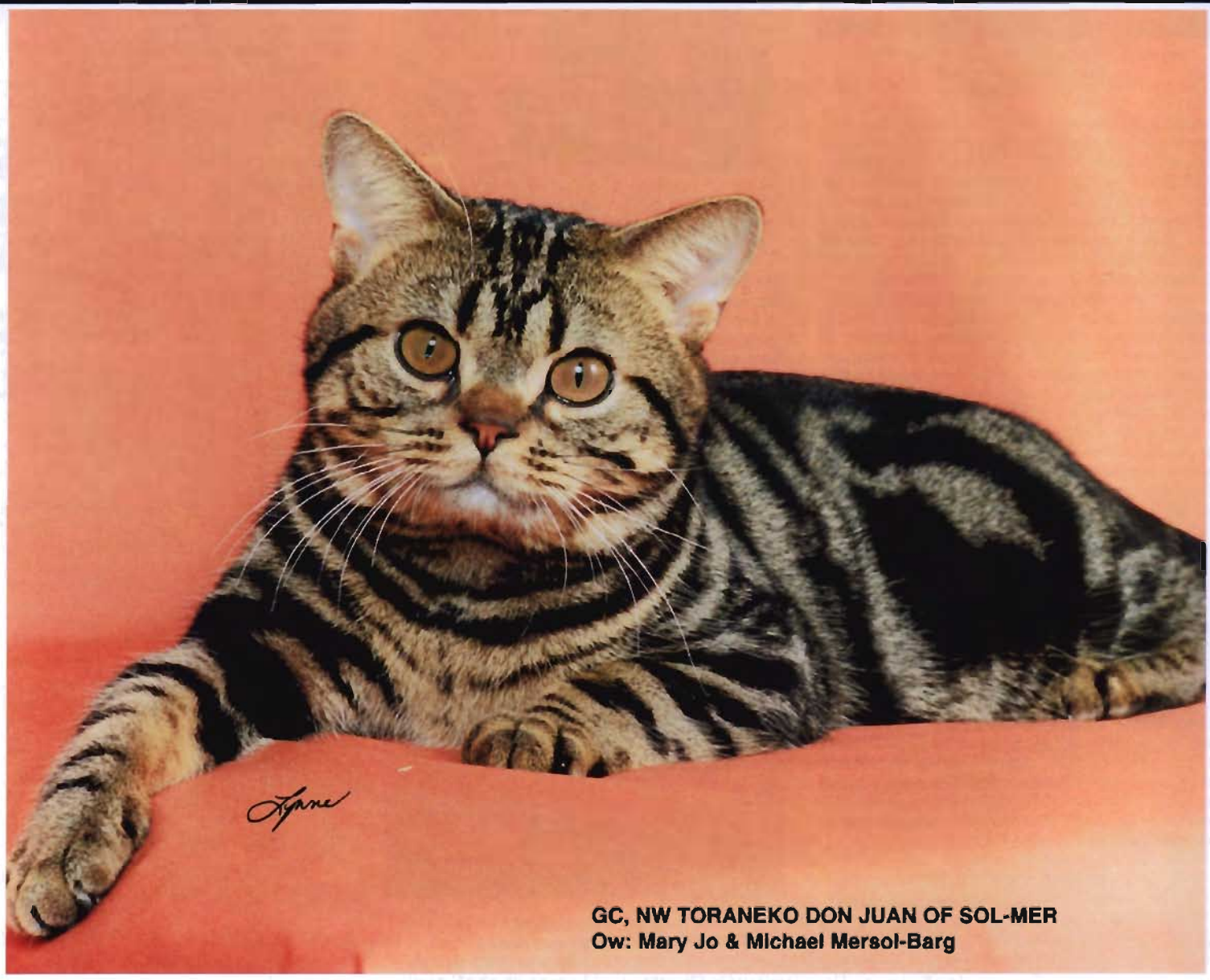
# *Variation on the Theme*

or

# HOW TO PAINT A CAT

## CAT COAT COLOR

*Heather E. Lorimer, Ph.D.*



**GC, NW TORANEKO DON JUAN OF SOL-MER**
**Ow: Mary Jo & Michael Mersol-Barg**

Several breeds, including my primary breed—the Oriental Shorthair (ORSH), have standards that allow for a multitude of coat color and pattern combinations. The sheer numbers of these colors can cause confusion on the part of breeders, exhibitors, and judges. Why are there so many colors? How can you tell them apart? How can you breed for a specific color? Breeding for color (along with type of course) can be fun and rewarding but it requires some understanding of what causes coat color and how it is inherited.

Many people work with breeds such as American Shorthairs, British Shorthairs, both types of Rex, and Maine Coon Cats, specifically to develop unusual colors. In fact the ORSH was created by Siamese breeders expressly for the purpose of painting the Siamese chassis in the full spectrum of colors. The ORSH breed standard actually states that "the Oriental Shorthair's reason for being is the coat color..". Aside from color, the ORSH is nothing more, or less, than a Siamese. Even so, the Oriental Shorthair does not allow some of the colors that other breeds allow. The actual count of colors and patterns listed in the ORSH standard is 53 as compared to the American Curl standard for instance, which lists 67 colors and patterns and also has a class for cats of any other color (OACC or Other American Curl Colors). The ORSH has no calico's, no bi-colors, no vans, and no "Other Color Class" for assorted oddly colored cats in championship. We currently do not accept

GC NW DOVON"S GOTTA LOVE IT DON'T YAH
Brown Tabby ASH Male
O: VonAswege

shaded goldens, and we unfortunately have no forum for our parental Siamese colors which naturally occur in ORSH litters. Nonetheless the ORSH, along with the other breeds that come in a multitude of colors, provide a real challenge for breeders who must first build their house (get type on their cats) and then try to paint it according to the exacting breed standards of CFA.

Detailed genetic information is very useful to people who breed any of the breeds that come in a number of colors. In terms of the nitty gritty of coat color genetics there are many articles and portions of books that describe genetics and color inheritance in detail, including an excellent genetics article by Rosemonde Peltz, M.D.,in 1992-93' CFA **Yearbook.** I would also recommend the section on genetics in "The Book of the Cat" by M. Wright and of course "Genetics for Cat Breeders" by R. Robinson, third edition. Unfortunately, if you have not had a good biology course recently, a lot of this information can be confusing and very difficult to apply to your immediate questions and needs. The March 1993 issue of the *Cat Fancier's Almanac* contained an article about Oriental Shorthairs written by Bob Agresta which concentrates on the rationale for the existence of such a multitude of colors as well as their names and descriptions. However, being able to name and describe colors is often not enough for those of us who breed these multi-colored cats. My purpose here is to bridge the gap between color descriptions and genetics. What exactly is the color? How did it get that way? How is it passed from generation to generation?

## THE BASIC CAT

The domestic cat is probably the descendent of a number of small wild cats . These cats are still able to breed with the domestic cat and produce viable offspring. The Scottish and European Wildcats (Felis Silvestris silvestris) and the Pallas cat from central Asia (Felis manul) are noticeably larger than the average domestic cat, while the African Wildcat (Felis Silvestris lybica) and Asian Jungle Cat (Felis chaus) are closer to the size of the domestic cat, a little smaller than their northern cousins. All of these small wild-cats have black tail tips and markings on a background color that ranges from cool beige through warm coppery colors to brown. This basic color range is also common to the big wild cats. The Cougar and the lion both have black facial markings and tail tips on a buff-tan background, the Leopard has black spots on a creamy gold background, the Tiger has black stripes on an orange to brick red background. Not surprisingly, this is also the most common color in our domestic cats. Your neighbor's cat "Tiger" has black stripes on a tan background that gives him an overall brownish appearance—thus he is called a brown tabby .

GC JO-NI SWEET ADELINE OF MEADOWOOD
O:Philpot and Dunn

This is the basic cat color and we have it in the majority of our breeds of pedigreed cats. In the cat fancy this color has many names: brown tabby (in many breeds including American Shorthairs and Persians), ebony tabby (in the Oriental Shorthair), ruddy (in Abyssinians),

GC FELITAN SILESTE
O: Richard and Barbara Felitan

tawny (in Ocicats), and bronze (in the Egyptian Mau)

What makes up this brown, or ebony, tabby? It is a cat with fur that has black "pattern" on a background, or undercoat that ranges from cream though copper to brown depending on the individual cat The lighter background color is inherited in a complex polygenetic fashion like skin color is with people, so it's hard to predict and control exact undercoat shades in a breeding program. Each hair on the cat has several "bands" of the darker and the lighter color on it. The actual tabby pattern is caused by the way these different hairs are clustered. You can think of this pattern as a set of fixed instructions on how the hairs are to be banded with color for each specific area on the cat's body. In some areas of the skin, the follicles make hairs that are mainly dark, while in other areas the hairs are mainly light. The tips of the hairs on the upper parts of the body are usually black. On hairs from dark areas, such as tabby pattern marks the black color can extend almost all the way to the base—fading only slightly to dark brown at the very base of the hair. On hairs from lighter areas between the tabby markings the hair has more bands of lighter than darker color. Hairs on the throat, chest, and belly of the cat are often colored only with the lighter "ground' or undercoat color, with the exception of any belly stripes or spots. The name for this banding of light and dark colors on the individual hairs on a cat is *Agouti*. The tabby pattern is as basic to the cat as two eyes and four paws. Every cat inherits and passes on tabby patterns, even if they are seal-point Siamese or solid blue Korats!

CFA recognizes four tabby patterns in various combinations among the breeds, classic (blotched), mackerel (striped), spotted, and ticked. Interestingly wild cats also have versions of these four tabby patterns. There are legions of spotted cats and striped cats. The Clouded Leopard and some European wild-cats have blotches and swirls similar to the classic tabby. Lions, Cougars, the Asian Jungle Cat and the Pallas cat are ticked.

All four of these tabby patterns are allowed in the Oriental Shorthairs. The classic tabby has wide swirls of dark color which form distinct bull-eyes on the sides . The classic tabby also has wider bracelets and tail rings than is seen in the other tabby patterns. The mackerel tabby has thin vertical stripes and narrow bracelets and tail rings . These two patterns are recognized in almost all the breeds that come in tabby. The Oriental Shorthair standard also allows spotted and ticked tabbies. Two CFA breeds, a very old one - the Egyptian Mau and a fairly new one - the Ocicat, are essentially purely spotted cats . The precise pattern standard for each of these breeds is different. The Egyptian Mau standard has very detailed requirements for the pattern on the cat's head and face and requires an unbroken spine line from the lower back to the tail tip. The Ocicat is more detailed on the placement, size, and shape of the body spots and requires spots all the way down the spine. The ORSH standard for spotted tabbies is not as detailed, although it does specify a preference for round, evenly distributed spots. Two other breeds, the venerable Abyssinian , as well as the Somali, and the recent addition of the Singapura , only come in ticked tabby. Abyssinians and Somalis must be completely free of barring while the Singapura must have some barring on the inner front legs and knees. The Oriental Shorthair ticked tabby standard requires even more barring, listing necklaces as well as distinct tabby striping on the face, legs and tail.

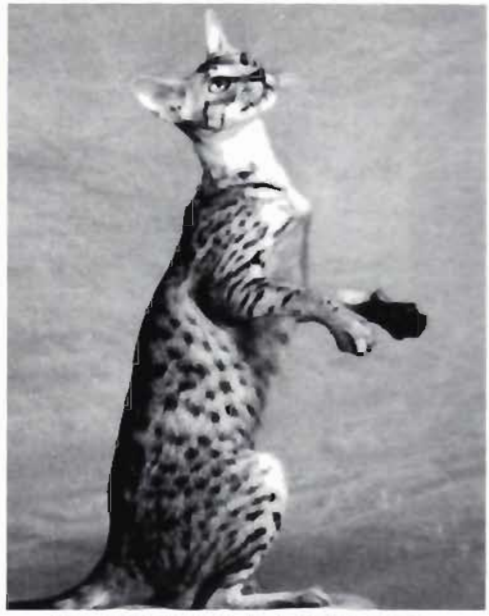
So, if the basic cat is a brown tabby, where did all the other colors come from?

## VARIATION ON THE THEME or HOW TO PAINT A CAT

How is a cat colored in the first place? As an analogy think of a house that needs to be painted. To paint the house you need paint, brushes and rollers, people to do the work, and some knowledge about house-painting or a very good set of instructions. However, unlike houses, cats inherit their color from their parents. Each cat get its color genes (for our purposes — instructions and paint) from its parents, one from its mother and one from its father. In this analogy this means two painters, each with complete supplies for house painting, one sent from Mom and one from


**GC BROCKHAVEN'S LA-DI-DOTS**
**Silver Egyptian Mau Female**
**O: Guerdon and Dorothea Brockson**

**GC NW ECHOES OF MAJA RUNNING BEAR SAGA**
**Chocolate Spotted Ocicat**
**O: Shana Kuhnert**



**GC FELITAN BOBBY JEAN OF KALAHARI**
**Ebony Silver Spotted Tabby**
**O: Lisa M. Greco**

Dad. Our basic cat painters, well supplied with brushes, rollers, detailed instructions and paint, use light warm brown for the sides and black for the trim, *i.e.*, our "house-cat" is a brown tabby.

Now in order for the color to change, the paint and/or instructions have to change. Each individual part of the paint and instructions has its own set of genes that control them. If these genes are changed than the color is changed too. A change in a gene is called a mutation. Mutations that cause visible changes, such as color or coat length, are very very rare.

Our cats coat colors come from mutations of the basic brown tabby. These are not new mutations. The few color mutations that have occurred during the several thousand year history of the domestic cat have managed to get spread all over the world. People like to keep unusually colored cats as pets and since cats have been living with us for so long it isn't too surprising that we have so many coat colors that have come from mutations from the original wild cat color. However, if you breed your Siamese queen to your lynx-point boy and get a solid ebony kitten, the odds are so overwhelmingly against a new mutation you can be sure that your girl was seeing another boy on the sly.

The most common cat color change among cats both large and small, is from tabby to the solid. This is the same thing that changes the Leopard to a Black Panther. How does this happen? Before painting the house it has no color, and in this case the absence of color is white. Think of the house painters, each arrived with the right instructions but somehow the paint order got mixed up and all they have is the trim color. However they feel they must paint the house anyway, so they paint all the trim black and then they paint the whole house black on top of that. This is where dominance plays a role.

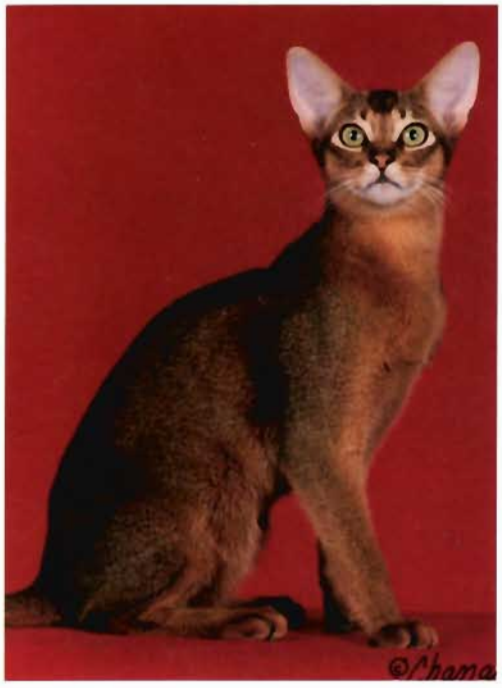
For the sake of this discussion some genetics terms need to be defined here. 1. A gene is a specific genetic element that controls a single trait, one gene is responsible for one protein, or one enzyme. 2. A locus is the location of the gene on the chromosome. Every gene has it's own locus. 3. An *allele* is one version of a gene, any given animal has two alleles of a gene, one from mom, one from dad. Sometimes one animal's two alleles are the same in which case they are homozygous for that allele, and sometimes an animal has two different alleles in which case it is heterozygous at that locus. 4. A dominant allele is seen, or expressed, even when only one copy of that allele is present. 5. A recessive allele is only seen when it is present in both copies, when the animal is homozygous. 6. The dominant allele is always capitalized and the recessive allele is lower case.

When it comes to painting cats the painters always have the instructions (tabby pattern), so if just one of the painters has the lighter color (brown) wall paint (provided by the *Agouti* gene dominant allele or *A*) the correct pattern is painted. Both painters have to have only trim color (the *agouti* gene recessive allele, *non-agouti* or *a*) for the whole house to end up black. Therefore the solid color is recessive which means that you don't see solid color unless both of the alleles are *a*. One important thing to remember about non-agouti cats is that it doesn't affect the cat's genetic pattern, it just removes the ability to color that pattern properly. So, when you breed a tabby to a solid you can unwittingly change the pattern that you get in your tabby kittens.

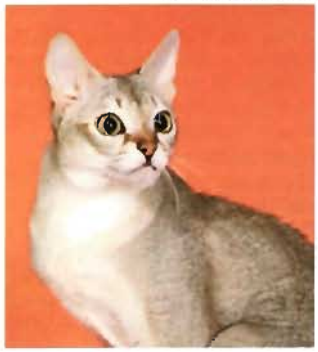
Cats come in many more colors than black or brown tabby. For our purposes let's temporarily abandon tabbies and just look at solid color cats. In solid colors there are three basic "trim paint" pigments (three alleles of the color gene) black (*B*), brown (*b*), and cinnamon ($b^1$). Most breeds call black black in solid colors, although ORSH call it ebony and Siamese call it seal. Siamese, along with Devon Rex, Ocicats and Persians call brown chocolate, while ORSH call it chestnut. Devon Rex, ORSH and Ocicats call cinnamon cinnamon, Siamese in foreign associations call it light chocolate, and Abyssinians call it red. What differentiates these colors is the shape and the thickness of the pigment granules on the hair. Black hairs result from thick round opaque color granules, chocolate granules are thinner and more oblong, and cinnamon are the thinnest and most stretched. These stretched granules are somewhat translucent which results in the warmer, lighter color. In the house-painters analogy the black paint is very dense and opaque, brown is less so, and cinnamon is less yet. If one painter paints everything black, and the other painter paints the same thing brown, the brown color will not cover up the black but the black will cover the brown. Thus, in terms of dominance, black is dominant to chocolate or cinnamon, similarly, chocolate is dominant over cinnamon.

Now for some real genetics. This particular set of colors presents an unusual case, there are three color alleles, and any given cat can only have two. Remember that each cat inherits one *allele* from its mother and one from its father. I will represent the alleles of a single cat here by the italic letter symbols for the alleles in parenthesis, separated by a slash. It is possible to have a black cat that is homozygous for black (*B/B*), or a black cat that is carrying chocolate (*B/b*), or a black cat that carries cinnamon ($B/b^1$). Since black is dominant all of these cats would appear to be the same color (black) but they are genetically different. For example if the homozygous black cat (*B/B*) was bred to a solid chocolate (*b/b*) or a solid cinnamon ($b^1/b^1$) all the kittens would be black because every kitten would get one *B* allele from the homozygous parent. If the black carrying chocolate (*B/b*) is bred to a chocolate cat (*b/b*), half of the kittens could be chocolate and half could be black. This is because each kitten would get one chocolate allele (*b*) from the chocolate parent and either a black allele (*B*) or a chocolate allele (*b*) from the heterozygous black parent. In the case of the black cat carrying cinnamon ($B/b^1$) an even more interesting thing happens when she is bred to a chocolate male. Again each kitten gets a chocolate allele (b) from its father, but in this case the other allele from mom is either black (B) or cinnamon ($b^1$). All the resulting kittens are heterozygous, either black carrying chocolate, or chocolate carrying cinnamon. A way to diagram this is shown in **box 1**. These boxes are called Punnett Squares and they show how the color alleles can be inherited from the mother and the father. On the top the mother's alleles are separated (remember each cat inherits one, and only one, pigment allele from each parent) and on the side is the fathers alleles. The central four boxes simply add the alleles from the mother and the father together. In the case shown in 1, there are only two colors (or phenotypes) of kittens and only two genetic (or genotype) results. Geneticists call the appearance of an animal its phenotype and its genetic makeup its genotype. In **box 1** the phenotype of the kittens is either black or chocolate and the genotype is either *B/b* or $b/b^1$.

In box 2 is a Punnett Square diagram of a slightly more complicated cross. Again the mother is black carrying cinnamon, but this time the father is a chocolate that also carries cinnamon. This produces all three phenotypes; black, chocolate, and cinnamon, and four different genotypes (*B/b*, $B/b^1$, $b/b^1$, and $b^1/b^1$). Unfortunately cats don't often produce four kittens, one of each possible phenotype and genotype. However, Punnett's squares do show the *probability* of producing a kitten of a specific color or genetic make-up, for instance the probability is 1 out of four or 25% for cinnamons in cross number two. Always remember that probabilities are true for only very large numbers. If the male and female from **box 2** had around 1,000 kittens, very close



GC TINBATS SEARCHING FOR CALEB
Ruddy Abyssinian Male
O: Reg/Lynn Martin



Singapura

to 1/4 of them would be cinnamon. If they had a litter of three they could very easily be all chocolates or two cinnamons and a black. Always remember that Mother Nature is

GC NANTASCOT COUGAR COUNTRY OF SUJONZ
Ebony Ticked Tabby OSH Male
O: Susan Zambroski

very capricious in the little things. If you are test breeding two cats to find out if they are carrying a recessive color, or any recessive trait, don't be too sure that you know the answer if the answer seems to be "no".

There is one more full pigment solid color, red. Red does not work like any of the other solid colors It is not another allele of the pigment genes mentioned above. Since it is a special case, I am going to discuss it separately from the other full colors.

## SEX and RED CATS

In one sense, red is another full pigment color, it produces pigment granules that are even more stretched out and transparent then cinnamon, producing a color that ranges from light yellow-orange to deep brick red. In a more technical sense the red gene is an independent modifier that changes the other three full colors (black, chocolate, and cinnamon) to red. Red is not another *allele* of the pigment color genes. It is very important to remember that a red cat also has two other full color alleles in some combination like those discussed above.

Red is inherited along with sex on the X chromosome. Red cats provide a classic example of sex-linkage of a phenotype and genotype. In fact, college biology and genetics courses almost always use red and tortoiseshell or calico cats as an example of how this kind of genetics works.

All mammals have two copies of each chromosomes, one of each chromosome from each parent, with the exception of the sex chromosomes X and Y. The X chromosome is a large and important chromosome with many genes on it. Females have two X chromosomes, but males have only one X chromosome and a very small chromosome to pair with it, the Y chromosome. The Y chromosome has only one really important function—it causes maleness. Offspring always get one of their mother's two X chromosomes and either their father's X or his Y. If the father's X is inherited the offspring is XX and is female, if the father's Y is inherited the baby is XY and is male. Therefore it is the father that determines the sex of his children.

This way of producing two sexes has a problem though. The X chromosome has many important genes on it but a male has to survive with only one X chromosome. The solution is for the X chromosome to be very powerful, so only one copy is needed to be completely normal (or at least normal for a male). This produces a second problem. If the X chromosome is that powerful, two copies are too much. Since females have two X chromosomes they have to inactivate one of the two in every cell in their bodies. This inactivation is done by the female embryo and is completely random. The female embryo grows, starting from a single cell—the fertilized egg— which divides repeatedly to produce many cells. At some point a message is sent, and received by all the cells, to turn off an X chromosome. When this message gets through the embryo has perhaps a few hundred cells and each cell independently turns off one X chromosome at random. This process is called X inactivation. After X inactivation each cell has only one fully functional X chromosome, the other X does remain in the cell for purposes of reproduction. Each cell, now with only one active X, continues to grow and divide, but all the cells descending from it has only that same one X chromosome active

Somehow the color red in cats is caused by a gene on the X chromosome. The X chromosome of a cat can either have the red gene ($X^O$) or not ($X$). Male cats have only one X, so they are either red or not. Males can have the genes to be black, chestnut, or cinnamon, but if they also have the red $X^O$ they are red. Since female cats have two X chromosomes they can be $X^O/X^O$, $X^O/X$ or $X/X$. If she is $X^O/X^O$ she is red, if she is $X/X$ she is not, but if she is $X^O/X$ she is both red and not red. If one X is red and the other one is not some cells will inactivate the red one and some will inactivate the other. The cells will then grow and divide

LITTERMATES
Ebony (black) and Ebony Silver Spotted Tabby

and when the kitten is born you can see the red patches that came from cells that inactivated the non-red X and the other patches where the red X was inactivated. Here is where you see the proof that red is caused by pigment modification because the tortie girl can be red and either ebony, or chestnut, or cinnamon . Wouldn't it be fun to see a tortie class with all the possible colors in it! The size of the patches of red depends on how early in development X inactivation occurred. Although it never occurs this early, if it happened after the first division, at the 2 cell stage, the cat could be half red and half black, split right down the middle! In fact it happens much later and results in very small patches of color and irregular larger patches. The patches are larger and often appear to be more symmetrically placed when the cat is also part white, i.e., a calico, but more about that later.

Since red color is on the X chromosome it is inherited along with the sex of the cat. This kind of inheritance is called sex-linked and follows its own rules, all of which make sense when you think about it. First, a male has only one X chromosome. All of his daughters inherit his X (they also get an X from their mother so they are XX, female). None of his sons inherit his X, instead they get his Y (and an X from their mother so they are XY, male). All of a female's offspring get one or the other of her two X chromosomes. Therefore a male cat has no influence on whether his sons are red or not because they do not get an X from him. On the other hand all of a red male's daughters will have his red X, and all of a non-red male's daughters must have his non-red X. Since a red female must have two red Xs, her father must be red, and her mother must have at least one red X— in other words a red female's mother must be tortoiseshell, calico, or red. If a female is red, all of her sons will be red and all of her daughters will be particolors or reds depending on their father's color. Examples of this kind of inheritance are shown in box 3 and 4.

The last unusual quality of red that I'm going to talk about here is its'

GC KEMAGE VICTORIA
Tortoiseshell OSH
O:Anne and Kevin Mathis

1.

| FATHER \ MOTHER | B | $b^1$ |
|---|---|---|
| b | B/b Black carrying Chestnut | $b/b^1$ Chestnut carrying Cinnamon |
| b | B/b Black carrying Chestnut | $b/b^1$ Chestnut carrying Cinnamon |

2.

| FATHER \ MOTHER | B | $b^1$ |
|---|---|---|
| b | B/b Black carrying Chestnut | $b/b^1$ Chestnut carrying Cinnamon |
| $b^1$ | $B/b^1$ Black carrying Cinnamon | $b^1/b^1$ Cinnamon |

pattern is not very strong, for instance bar-less ticked tabbies in shorthairs or poorly marked mackerel tabbies in longhairs.

For show purposes it doesn't matter if a red tabby is a genetic tabby or a genetic solid, red tabbies are judged on appearance not genotype. For breeding purposes there are a couple of keys to help determine if a red tabby is a true agouti tabby (*A/A* or *A/a*) or is a non-agouti solid (*a/a*). Ancestry is always the easiest key to a cats genetic makeup, if a red tabby male's mother is a tortie and his father is black, then he must be non-agouti (genetically solid colored) since both of his parents are non-agouti (*a/a*). If ancestry doesn't provide a clue (for instance if mom is a tortie and dad is a brown tabby carrying solid color) than there are some visual clues to look for. A true tabby almost always has a white chin, white whiskers, and white markings outlining the bottom parts of the eyes. In a non-agouti red tabby these areas are a lighter color red, not white. The red tabby ORSH shown here could be easily guessed to be non-agouti due to the redness of her chin and throat.

You've probably noticed that in all my discussions of red I haven't mentioned cream, which is another possible color that can come from red or tortoiseshell cats. The reason is that cream is a dilute color and I haven't talked about dilutes!

*Roses are Red,*
*Violets are Blue,*
*Blue cats are Gray,*
*Which is Black gone Dilute*

3.

Red Father

| Black Mother \ | $X^o$ | Y |
|---|---|---|
| X | $X X^o$ Tortie | X Y Black |
| X | $X X^o$ Tortie | X Y Black |

4.

Red Father

| Tortie Mother \ | $X^o$ | Y |
|---|---|---|
| $X^o$ | $X^oX^o$ Red | $X^oY$ Red |
| X | $X X^o$ Tortie | X Y Black |

5

Chocolate Male
(b/b, D/d)

| Blue female (B/b,d/d) \ | b, D | b,d | b,D | b,d |
|---|---|---|---|---|
| B,d | B/b D/d (black) | B/b d/d (blue) | B/b D/d (black) | B/b d/d (blue) |
| B,d | B/b D/d (black) | B/b d/d (blue) | B/b D/d (black) | B/b d/d (blue) |
| b,d | b/b D/d (choc.) | b/b d/d (lilac) | b/b D/d (choc.) | b/b d/d (lilac) |
| b,d | b/b D/d (choc.) | b/b d/d (lilac) | b/b D/d (choc.) | b/b d/d (lilac) |

Dilute is another completely different gene that changes the appearance of all the colors mentioned above. Sometimes the house painters arrive, with all their instructions and equipment, but their brushes aren't very good. The paint doesn't stick to them well and the bristles keep separating. The paint goes on in irregular streaks leaving lots of white showing through. From a distance the house that was supposed to be brown with black trim ends up closer to buff with gray trim. This is dilution, which is controlled by a completely different gene than the pigment genes mentioned above. This gene has two alleles, full, dark color (*D*), and dilute (*d*). Full color is dominant to dilute, one coat of a good paint job can cover up the bad paint job, so a cat must have both dilute genes to be dilute. What really happens is that the amount and distribution of the pigment granules is changed, causing layers of irregular rings of pigment on the hairs with unpigmented areas between. It is unmistakable under a microscope that is lit from above. To the naked eye the color appears to be lighter and duller. This changes the appearance of all the pigments, black becomes gray (ebony to blue), chestnut changes to lilac or lavender, cinnamon becomes fawn, and red lightens to cream.

A lot of breeders confuse dilution with the different full pigment colors. Chocolate is not a dilution of black (or seal or ebony), chocolate is a full color. Blues do not carry black, blues are the dilution of black. Lilacs are not a further dilution of blue, they are a dilution of chocolate. Dilution produces the color that you would expect if you mixed pale gray with the full color pigment. Since pigment and dilution are separate genes they can mix and match in unexpected ways. It is possible to get blacks, blues, chocolates and lavenders from a blue bred to a chocolate. It is also possible to breed a chocolate to a blue and get a litter of nothing but blacks!

"Transparency". All cats have a tabby pattern. If a cat is solid colored it's because the lighter color can't be painted or banded onto the individual hairs. As the full colors get lighter and hotter from black to chestnut to cinnamon to red the pigment granules become elongated and more transparent. This causes the underlying tabby pattern to be more visible in a genetically solid colored (*a/a*) cat. In the house painter analogy the solid color house painters do the trim first, and then do everything with another coat of paint. This results in more coats of paint on the trim then is on the walls. When the pigment is very heavy (black) it covers very well with even a single coat and the cat is black. When the pigment is very thin (red) it doesn't cover with a single coat and the color difference between the trim and walls is very pronounced. The end result is that almost all red cats appear to be tabbies, even those that are genetically solid colored. Cats that appear to be solid red only happen when the underlying tabby

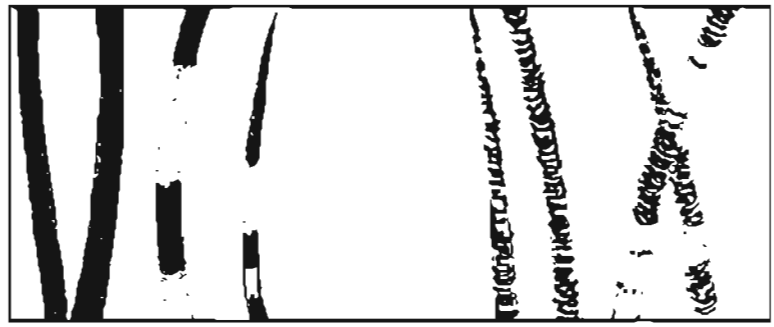
GC PRINTERS SWEET ROSIE O'GRADY
Red Tabby OSH
O: Ann and Bob Sumrall

A chocolate or chestnut must have both chocolate pigment genes and one full color gene to be chestnut. A blue must have both dilute genes and one ebony gene to be blue. If a chocolate male has one dilute gene and the blue female he is bred to has one chocolate gene then the litter can arrive in all four colors. If this is the case, each kitten will get one chocolate gene from its' father, and either a black or a chocolate gene from its' mother so roughly half of the kittens will have two chestnut genes. Each kitten will also get one dilute gene from the mother, the other will be either the fathers full color or his dilute so roughly half of the kittens will be dilute. The inheritance of two separate genes can also be diagrammed in Punnett's squares as show in box 5. In cases like this, with more than one gene, each combination of single genes from one parent are written across the top or the side of the boxes. Since there are two genes each with two alleles there are 2 X 2 or 4 different combinations to inherit from each parent. It doesn't matter if the alleles of a gene are the same (homozygous) or different (heterozygous) they count as two alleles. Remember that the individual phenotype can be counted up in the Punnett square to estimate the likelihood of a kitten coming out a specific color. In terms of probability the most likely ratio would then be 1/4 ebony, 1/4 chestnut, 1/4 blue, and 1/4 lavender.

Sometimes when a chestnut is bred to a blue all the offspring are ebony. In this case the blue is probably homozygous for ebony as well as dilute, and the chestnut is homozygous for both chestnut pigment and full color. The resulting kittens are therefore heterozygous for both pigment color and for dilution (B/b, D/d). Since ebony pigment and full color are dominant all the kittens are black.

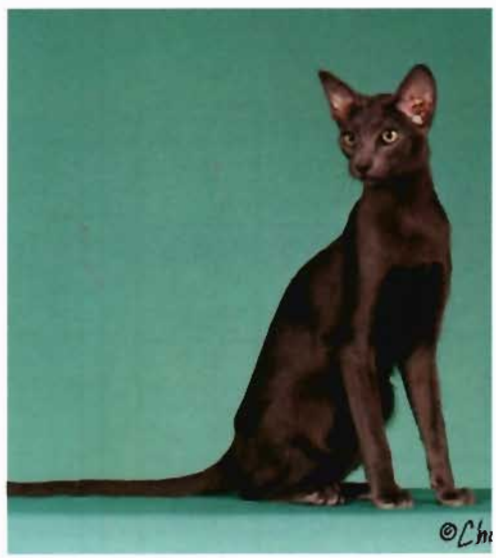
Remember that ebony and chestnut, as well as cinnamon and red, are pigment color genes. Blue, lavender, fawn, and cream result from dilution of the pigment color genes. All ebony, chestnut, cinnamon, and red cats have full color (phenotype) and at least one full color gene (genotype). All blue, lavender, fawn, and cream cats are dilute (phenotype) and have two dilute genes (genotype).

Phenotype is a scientific word that means outward appearance, genotype is the actual genes that the organism (read cat) possesses. In other words phenotype is what you see and genotype is what you get. Determining your cats phenotype is easy (usually) but the cats genotype can only be told by examining the phenotype, the pedigree, and most importantly the cats offspring. If your ebony (black or seal) cat had a lavender (lilac) mother then you know a good deal about your cats genotype. Being ebony, she must have one ebony gene and one full color gene. Her mother was lavender which is the dilute of chestnut (*b/b, d/d*) or (*b/b*$^1$, *d/d* )—but since the cinnamon gene is still rare assume two chestnuts here. Therefore your ebony girls' other pigment gene is chestnut, and she also has one dilute gene. A breeder might say that she "carries" all four colors.



DRAWING OF A MICROSCOPIC IMAGE OF CAT HAIRS ON THE LEFT SOLID BLACK AND BROWN TABBY HAIRS. ON THE RIGHT BLUE AND BLUE TABBY HAIRS

GP NW SAN-TOI ORIENT EXPRESS OF ELSK
Ebony (black) OSH
O: Lynda and Don Campbell



GC PURRTEECATS STORMY SKIES
Blue OSH
O: Robert and Sharon Gummow

Confused yet?

There are four other modifying genes that effect cat color. One is the alleles of the albino gene. The normal color allele is dominant (C) the albino allele (c) is very rare in cats but there are other recessive alleles of this gene which are very important in the Cat Fancy. First is the Siamese gene ($c^s$), which is what we scientists call a temperature sensitive mutation. It is a recessive gene and affects the placement of pigment. In this case the house painters won't work when it gets too hot. In areas where the cats skin surface is cool, like the nose, ears, tail and feet, the pigment is normal. In warm areas, like the body, throat, and eyes, the pigment is not made very well, if at all. Thus the cat is blue eyed and pointed, dark at the extremities and very light on the body. This also explains why pointed kittens are born white; its very warm in the womb so no pigment is made . As Siamese (or Balinese, Birmans, Colorpoints, Himalayans, or Javanese) age,their blood circulation to the skin decreases, the skin temperature drops and the whole cat gets darker. The second modifier is another temperature sensitive allele ($c^b$) but it is much less affected by temperature. This results in color that is dark on the extremities, like the Siamese, but lightens only slightly on the body, changing black to the rich sable brown of the Burmese. The show Tonkinese must be heterozygous ($c^s$, $c^b$) to produce the intermediate color and aqua eyes required by their standard.

The second gene is silver, which is dominant and effects only the undercoat, not the pattern color. This gene causes the background or "wall" color to be completely eliminated. Its as if the house painters are using clear gloss for their wall paint. All tabbies are changed by silver to silver tabbies. Many breeds recognize the black silver tabby, which is commonly called a silver tabby by default. These breeds also recognize the red silver tabby, which is called cameo tabby and therefore the combination, patched silver tabby in females. A few breeds, including the Oriental Shorthair, Ocicats, and Devon Rex include all or the majority of the other tabby colors in silver These colors are named according to pattern (or trim) color, then ground (or wall) color, and finally specific tabby pattern . So, if a cat has both chocolate genes (*b/b*), both dilute genes (*d/d*), at least one silver gene (*I/I*, or *I/i*), and is a spotted tabby, it is a lavender silver spotted tabby!

Silver also effects the undercoat color of solid colored cats. The hairs of a non-silver solid have roots that are a little lighter than the tips. If the genetically solid (*a/a*) cat is a silver those roots become silver-white instead of just a little lighter. These cats are called smokes The depth of the white band at the root of the hair for both silver tabbies and smokes is probably determined by many genes, which get descriptively lumped together as "banding". A wide banded smoke has a deep white undercoat, often showing through to the surface more than is desirable in most smoke color standards, which requires the cat to appear solid colored in repose. The wide-banded smoke also reveals its underlying tabby pattern (remember, all cats have tabby pattern). This is taken advantage of by the Egyptian Mau standard which emphasizes pattern and wants those spots to be visible. In contrast, a narrow banded smoke is very solid in appearance and has only a tiny band of white at the base of the hair, this cat may not even appear to be a smoke at first glance and requires careful examination to be sure of the color. Some smokes have a very charcoal-like grayed appearance without a wide band of silver at the base of the hair shaft, with the underlying tabby pattern clearly apparent. I

don't know what causes this, perhaps the banding cut-off is vague in these cats, or maybe it is simply due the coat texture being finer and more transparent by nature. In any case it is not uncommon and is annoying because, like the wide banded smoke, these cats do not really meet the common smoke color standard.

## A SMOKY PAST and A SHADY FUTURE

Many ticked tabbies are narrow-banded which means that there are many bands of light and dark pigment between the tip and the root of the hair. The Abyssinian breed standard prizes narrow-banding and the resulting increased number of bands of ticking. Wide-banding spreads out both the light and dark bands and reduces the number of color changes on one hair. Very wide-banding leads to hairs that only have color on the very tips of the hairs which causes the cat to be very light in color compared to a narrow-banded cat.

**LITTER OF OSH KITTENS**
**24 hours old including 2 pointed ($c^s/c^s$) kittens**

Very wide-banded cats with faint tabby patterns appear to be a shimmery shaded gold or rust, unless they're silver, in which case they have a very characteristic sparkling appearance. Shaded silvers and goldens are tabbies! At one time it was thought that a shaded silver was a very pale smoke. However, as anyone who has ever bred smokes can tell you, the paler the smoke the greater the contrast is between the darker face and legs where the hair is shorter, and the lighter body where the white under coat is more visible. A shaded silver is exactly the opposite, the legs are very white and the body is darker. It seems that to be shaded a cat needs to be a wide-banded tabby with very little visible tabby pattern. The wide-banding makes the silver cat very pale, and makes the non-silver very golden, with very little pattern (or trim) color. The way most breed's color standards are written, cats with defined leg and tail barring are tabbies, not shadeds regardless of the band width. On the other hand these standards do not rule out ticking or dark color on shaded silvers, although the paler wider-banded shaded silver is more attractive.

In trying to produce shaded silvers in Oriental Shorthairs I noticed some interesting things about tabby patterns. It seems that ticked tabbies either have defined stripes on their legs and tail or they have virtually none. My first shaded cat appeared unexpectedly out of a normally marked lavender ticked silver tabby and a pale smoke with no discernible pattern, two of the kittens were smokes, one was a spotted silver tabby and one was shaded. Since we had no idea what underlying pattern the father was, I did an experiment. I wanted to create another shaded silver. I had a ticked pattern lynx-point

**Litter of OSH kittens, 3 months old showing color development of pointed kittens and variation in ground color on ebony tabbies**

queen who could have been a silver. My shaded male had died tragically young, leaving no offspring. I wanted to find a patternless cat to breed my girl to and I found one although he was non-agouti. Remember that only solid colored cat that has a truly visible pattern is a red or a cream. I obtained a solid cream male with absolutely no barring and bred my girl to him. She produced two normally marked tabbies and two barless, ringless kittens both blue males. I have since observed several breedings between a barless ticked tabby and a barred ticked tabby and roughly 50% of the resulting kittens are barless. Barless kittens can also come from breeding two barred ticked tabbies, but not from breedings where one parent is spotted or mackerel. This implies that a barless tabby may have to be homozygous ticked. My next question is are all homozygous ticked cats barless? If you know the answer and have the proof please let me know!

The last two color modifiers are white and white spotting. White and white spotting are the result of at least two independent genes although they have some common traits. These genes are dominant and cover all other colors and patterns.

## WHITE-OUT for FELINES

Back to the house painter analogy, the house is white before it is painted. Sometimes the house is treated with the wrong weatherproofing when it is built. The two painters arrive with all their paint and instructions but the paint just won't stick to the surface. The house stays white. Sometimes this inability to hold color even extends somewhat to the eyes causing them to be odd-eyed or blue-eyed. To add to the confusion, some blue-eyed whites are blue-eyed not because they are white but because they have the Siamese color genes ($c^s/c^s$) under the white. There is no way to tell what colors a white adult cat would have been except by the colors of any non-white ancestors and offspring. As kittens though, sometimes not all the paint has fallen off yet. A tiny patch of color on top of the head can tell you what color the cat would have been if she wasn't white. I have even seen people guess (correctly) that a blue-eyed white Oriental Shorthair was a lynx-point underneath the white, based on a little colored spot on top of the kitten's head!

White color in cats is associated with deafness. "Deaf" white cats are born hearing but become deaf soon after birth. If the kitten is a homozygous white (both alleles are white), or is blue eyed without being Siamese colored underneath the white, the chance of deafness seems to be greatly increased. Heterozygous white (one white gene, one not) kittens are only very rarely deaf, so people who breed white cats often avoid breeding whites to each other.

White-spotting is also dominant but the amount of white on the cat is effected by whether the cat has one or two copies of the gene. Van patterned cats, which have color only on the head and the tail are homozygous for white-spotting. Bi-colors that are 50% or less white are usually heterozygous for white-spotting. It is currently thought that there are either two different white spotting genes or more than two different alleles of one white-spotting gene. A pattern called "tuxedo" is common in domestic cats, producing white spotting restricted to the feet, throat, and belly, which is a great deal less than is on the heterozygous bi-color. Birmans are usually homozygous for their variety of white spotting and yet have very restricted amounts of white. It's possible that the Birman pattern is related to the domestic cat's "tuxedo" pattern and that this may be a separate allele of the white-spotting gene. This is now referred to as "gloving".

White or white spotted cats that are white around the eyes are sometimes blue-eyed even if they are not pointed ($c^s/c^s$). Sometimes they are odd-eyed. Oddly enough, odd-eyed cats are much more likely to be deaf in the ear adjacent to their blue-eye than in the other one. Solid white is known to be a separate gene from white-spotting as it can cover white spotted colors like bi-colors and calicos. In fact, odd-eyed whites used to be AOVs in Oriental Shorthairs because it was assumed that the odd-eyes came from the cat being a bi-color underneath the white, and bi-colors are not accepted in ORSH in CFA. It has since been proved that white kittens resulting from breeding a white to a non-white oriental may be odd-eyed even though none of the ancestors or non-white kittens in the litter are white spotted.

Another oddity of white spotting is that it appears to affect the timing of X-inactivation in the female embryo. Tortoiseshells without white, or with only white gloving have much smaller patches, which are often irregular or brindled. Calico and van-calico or Mi-Ke cats, which have one red $X^o$ one non-red X and white spotting, have large unbrindled patches of red and black. The only way the patches of red and black could get so large and clear is if X-inactivation occurred earlier in the development of the female embryo in white-spotted cats. It would be interesting to find out if solid white effects X-inactivation as gloving apparently does not.

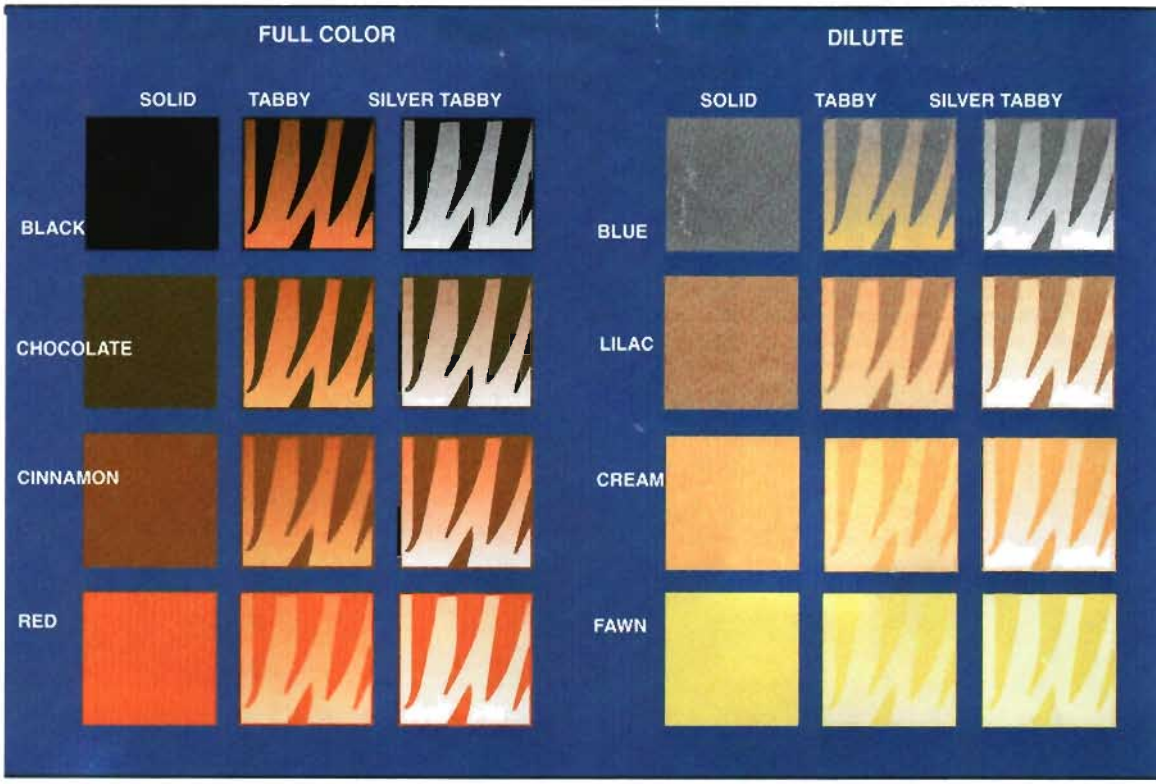
## BACK TO THE BASICS

Currently the inheritance of the tabby patterns is not well understood. Most theories that I have seen in print are at least partially incorrect. For that reason I won't use the standard symbols for the tabby genes because they are misleading. What is usually true in most cat-color genetics articles is that the ticked pattern is dominant to all the others and that classic is recessive to mackerel. However, it is still largely unknown that all the tabby patterns are not alleles of the same gene. In other words there are at least two separate genes that control

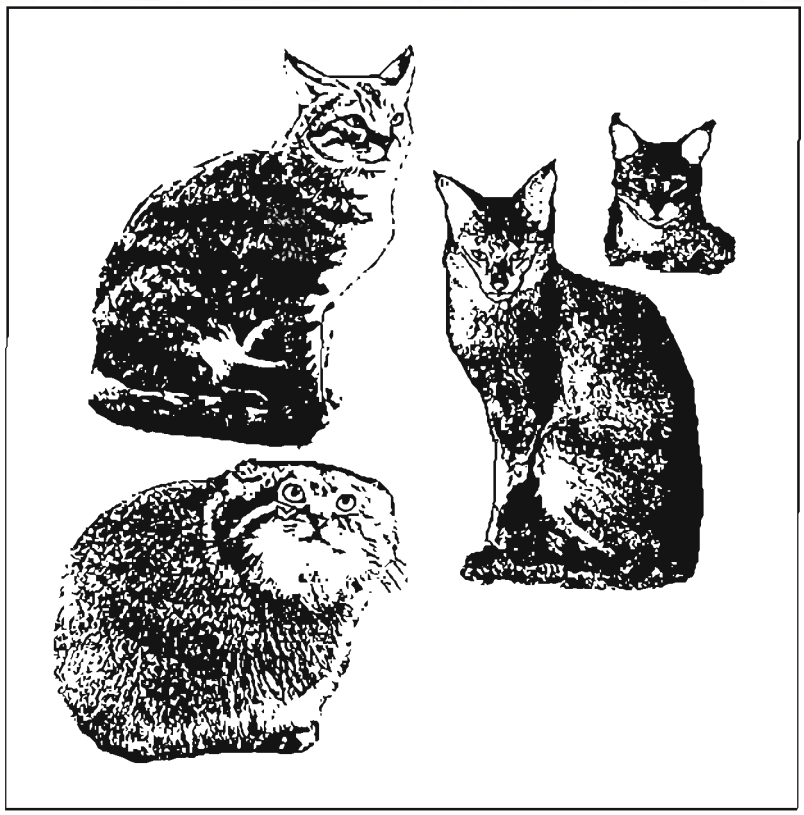
pattern, if not more. For instance, it is possible to breed two ticked tabbies together and get ticked, spotted and mackerel kittens in the litter. Previous published articles on genetics assume that all the different patterns result from alleles of a single gene, with classic being the most recessive and the litter I just mentioned would be impossible if that were true. With ticked being dominant and each parent having one ticked "allele" there would only be one non-ticked option, the result of the combination of the two parents non-ticked "alleles". Therefore, it would not be possible to have two different non-ticked patterns in the litter. So, there must be more than one gene controlling tabby patterns.

My current theory is that classic and mackerel are alleles of one gene (mackerel dominant), ticked and non-ticked are alleles of another (ticked is dominant), and finally spotted or not-spotted being alleles of a third gene. I have noticed that spots usually fall either into mackerel rows or classic dots surrounded by circles of dots. Maybe spotting modifies underlying mackerel or classic pattern. Spotting appears to be dominant to non-spotted as Ocicat litters out of two spotted adults sometimes have classic tabby kittens. If this is true then the spotting gene must be so prevalent among Oriental Shorthairs that a large percentage of spotted ORSH are homozygous for spots. The evidence for this is that spotted tabbies are common in ORSH and a number of these spotted tabbies have classic pattern spots but classic tabbies are very rare in ORSH.

However, there may be more than one genetic way to become spotted. Some American Shorthair breeders assure me that it is possible to get spotted kittens by breeding a classic to a mackerel tabby. This is a problem for these breeders as the ASH standard, unlike the British Shorthair standard, does not include spotted tabbies. This information may be somewhat confused by the fact that mackerel pattern spotted cats often have some spots joining together to form lines and an ASH with a broken mackerel pattern would surely be registered and shown as a mackerel. I am currently trying to collect information on the patterns of kittens out of two tabby parents. I have done a reasonable number of tabby to tabby breedings in my ORSH program but so far all the cats that I have used were either ticked or spotted and all the resulting kittens have been ticked or spotted although the spotting patterns have varied widely. I would appreciate any information that anyone else could add to this or any of the genetic theories in this article. I can be reached by writing to Dr. Heather E. Lorimer, 4758 2nd Ave NE, Seattle, WA 98105.




**ABOVE: COLOR CHART SHOWING THE FULL COLOR AND DILUTE COLORS IN SOLIDS AND TABBIES**



**Clockwise from upper left. The African wild cat *Felis Silvestris lybica*, the Asian jungle cat *Felis chaus*, Pallas' cat, *Felis manul*.**

*About the Author: Heather E Lorimer Ph D (Synergy Cattery) was born in Oakland, CA in 1957. She grew up in California, and later, Eugene Oregon. She earned her Bachelors in Biology at the University of Chicago, and M.A., M. Phil, and Ph D. degrees in Biology, specializing in virology and molecular biology at Columbia University in New York City. Shortly after she moved to New York, in 1982, and was introduced to the world of pedigreed cats by the Stalcup family (Temeluphil). Specifically a little blue-silver spotted tabby Oriental Shorthair kitten (Temeluphil's Thromboxane of Synergy) decided that Heather was his. Shortly thereafter Judy Thomas turned her into a clerk, and Barbara Levitan turned Heather into a breeder. She has been active in Oriental Shorthairs of America since its very first meeting, writes genetics articles for the OSA newsletter "Tails of the Orient" as well as the Cat Fanciers Newsletter and has given seminars on cat genetics. Heather put together a feature article on the Oriental Shorthair for the 1992 CFA yearbook (with a 1996 update in progress). She has also written a number of articles about DNA replication (not in cats) for peer reviewed scientific journals. Heather is also a board member for OSA and the new Oriental Longhairs club. She was active in the Empire Cat Club when in New York. Heather now lives in Seattle and is a member of the North Pacific Siamese Fanciers, and is engaged in post-doctoral research in the Department of Genetics at the University of Washington funded by a fellowship from the American Cancer Society. Her breeding program currently focuses on shaded silver Oriental Shorthairs.*

**Some DEFINITIONS**

**Allele:** a version of a gene.
**Chromosome:** a very large piece of DNA with many genes strung together, visible under a high power microscope. Mammals have two of each chromosome except the X chromosome in males who are XY instead of XX.
**Dominant:** an allele which is visible or obvious in some way when there is only one copy.
**Gene:** a unit of inheritance, technically a specific region of a chromosome that codes for a single protein or enzyme.
**Genotype:** the genetic makeup of a living organism.
**Heterozygous:** having two different alleles of one gene.
**Homozygous:** having two copies of one allele of a gene.
**Phenotype:** the appearance of a living organism.
**Recessive:** an allele which must exist in two copies to be visible or otherwise apparent.

EBONY (BLACK) SMOKE OSH KITTEN