

The sex-linked black cat fallacy: a textbook case

W. J. Miller and W. F. Hollander

ABSTRACT: Textbook presentations of the genetics of coat color in cats are compared with research literature on cat genetics. There is general failure of the textbook authors to identify mutants by contrast with wild-type standard, thus leading to the erroneous conclusion that black is sex-linked and allelic with yellow.

THE GENETICS of domestic cats is almost as popular as that of *Drosophila*, and Roy Robinson's³⁹ book "Genetics for Cat Breeders" has been its Bible for 15 years. There have been numerous published scientific studies, notably in the *Journal of Heredity*^{20,27,52} and the tortoiseshell or calico cat has been a recognized example since about 1962 of the 'single active X-chromosome' or Lyon hypothesis for female mammals.

But a schism exists between the research reports and many textbooks of genetics in regard to black cats: the textbooks typically say that black is sex-linked, while the cat geneticists do not. We have been intrigued by this contradiction, and have surveyed some three dozen texts in an attempt to understand the basis.

For convenience, we divide the textbooks into three groups: 1) those published up to 1950, 2) those between 1950 and 1975, and 3) those of the last decade. A few texts in their several editions bridge these groupings.

Group 1: to 1950

The first comment we have found was in Bateson's⁵ book (1909, p. 120 and later editions). Doncaster's early work is cited, with the conclusion that "the female heterozygote of orange X black is tortoise-shell." Plate's³⁵ 1913 text (p. 244) states that males are either orange or

black. His second edition published in 1933 (p. 894) is explicit: black and yellow are allelic and X-linked, and the heterozygous female is tortoiseshell.

Sirks⁴⁵ (1922, p. 256 and in later editions) considers black and yellow as sex-linked but not allelic, with symbols *B* and *Y*, respectively. Walter⁵⁴ and Sinnott and Dunn⁴⁴ have nothing on cat's colors until their final editions, much later, where they follow Plate. Snyder⁴⁷ (1935) seems to be the first American textbook author to present the matter (p. 68): "In cats, a factor for yellow is allelomorphous to one for black, and they are carried on the X-chromosome." By the second edition (1946, p. 91) he assigns the symbols *B* to yellow, *b* to black, and *Bb* to tortoiseshell. Darlington and Mather¹² (1949, p. 40) essentially follow Snyder. White⁵⁵ (1940) does not consider cat colors.

Colin⁸ (1941) does not follow either Plate or Snyder. He states (p. 44): "In cats, solid black fur (*aa*) is recessive to wild, tiger pattern (*AA*)," without sex-linkage.

Group 2: 1950-1975

Crow¹⁰ (1950, p. 17) says "In cats the genotype *BB* is black. *Bb* is tortoiseshell, and *bb* is yellow. The gene is on the X-chromosome." In his seventh edition (1976, p. 34) he is more cautious: "tortoiseshell cats . . . are heterozygous for an orange color gene. The orange spots contain cells where the dark color gene is inactivated, and the dark parts have the orange gene inactivated" (Lyon hypothesis). Winchester⁵⁷ (1951, p. 126) says: "In cats there is a gene for coat color which is intermediate [i.e., incomplete dominance] and sex-linked. There is one gene for yellow and one for black." In his 4th edition (1972, p. 182) he brings in the Lyon hypothesis to explain the tortoiseshell or calico females and specifies: "They are heterozygous for yellow and black." Srb and Owen⁴⁸ (1952, p. 97) use the symbols *y* for yellow and *Y* for black, with *Yy* being the tortoiseshell females. Bamber⁴ (1927) is cited as authority. Their second edition (with Edgar) agrees. (Unfortunately, Bamber's symbols were the reverse: *Y* for yellow, *y* for "extension of black.")

Dodson¹³ (1956, p. 81) says: "In cats, the gene *B* subserves yellow coat color, while its allele *b* subserves black," *Bb* being tortoiseshell. He thus follows Snyder, rather than Crow.

King²⁸ (1962, p. 110) indicates that black and yellow are sex-linked alleles, and in his second edition he uses symbols *B* and *b*, like Crow. His "Dictionary"²⁹ agrees.

Singleton⁴³ (1967, p. 221) says cats have a (sex-linked) "gene pair causing black or yellow hairs." And on p. 558 again he says: "The gene for black and yellow is sex-linked." He follows Crow in assigning *B* for black, but uses *Y* for yellow, as did Sirks. A male yellow then is symbolized *Y*—(the Y-chromosome a blank), a bit confusing for the student!

Gardner¹⁷ (1964, p. 111) states: "The alternative black and yellow pigments . . . have been associated with a pair of sex-linked alleles." They certainly had been. However, in later editions he avoids mention of these cat colors.

Hutt²⁴ (1964, p. 143) follows Crow: "Black and yellow coats in cats are determined by the sex-linked alleles *B* and *b*." However, the second edition (1982) grudgingly changes the symbols to *o* and *O*, with reference to Robinson.

Serra⁴² (1965, vol. 1, p. 109) mentions "the yellow-black pair of alleles" as sex-linked.

Strickberger⁴⁹ (1968, p. 478) follows Srb and Owen, symbolizing the alleles *Y* for black and *y* for yellow. But then on p. 707, in reviewing a gene-frequency report by Todd, he says: "In the heterogametic XY males, the presence of the yellow gene produced yellow fur, while its normal allele (*y*⁺ or simply +) produces a darker color whose particular shade and pattern depends on the presence of other genes." His later editions give the same information. Should the student be blamed for concluding that there are 3 alleles (*Y*, *y*⁺ and *y*)?

Goldschmidt¹⁸, Goldstein¹⁹, and Herskowitz²¹ do not commit themselves on black cats. Also Burns⁷ (1969 and subsequent editions) leaves this point untouched.

Group 3: 1975-1985

Merrell³² (1975, p. 110) starts this decade out with a throwback to Plate—*b* for black and *B* for yellow. He adds the significant comment: "In cats, black is unlucky." Farnsworth¹⁶ (1978) doesn't push his luck—nothing on black cats.

Avers² (1980, p. 103) says: "in cats there is an X-linked gene governing black or orange fur color. Males are either black or orange." Wagner et al.⁵³ (1980, p. 112) say: "a pair of alleles, *B* and *b*, appear to be sex-linked in cats. In females *BB* gives black coat color, homozygous *bb* gives yellow, while the 'hybrid' animal (*Bb*) is the familiar 'tortoiseshell'." This evidently is a throwback to Crow's earlier editions.

Suzuki et al.⁵¹ (1981, p. 99) say: "male house cats are either black or yellow" but use no symbols. Redei³⁷ (1982, p. 118) changes the wording: "Male cats can be either yellow or black." Klug and Cummings³⁰ (1983) and Ayala and Kiger³ (1980, 1984) do not get into cat colors. Brewer and Sing⁶ (1983) mention the tortoiseshell cat only as an example of the Lyon hypothesis.

Elseth and Baumgardner¹⁵ (1984, p. 230) say: "In the house cat (*Felix domesticus*) [sic], coat color among females can be yellow, black, or tortoiseshell," sex-linked alleles. L. A. Snyder et al.⁴⁶ (1985, p. 59) say: "The black and yellow pigments in the coats of cats are determined by an X-linked pair of alleles. Males are either black or yellow." They use novel gene symbols: *c^b* and *c^y*.

Discussion

Despite the chaos of symbols, the near-consensus of textbooks (except Colin) that black and yellow (orange) are alleles seems to indicate that the authors tend to follow one another in preference to the technical literature. In this case, the source of the error seems traceable to Bamber's⁴ review (1927), or rather to incomplete reading of the study. She was using the terms orange or yellow and black following pre-

The authors are, respectively, professor, and emeritus professor of genetics, Iowa State University, Ames, Iowa, 50011. Journal paper no. 79, College of Agriculture, Iowa State University, Ames, Iowa 50011.

© 1986, American Genetic Association.

vious authors and their symbols: Little (1912) does not refer to wild type, but Doncaster (1913, p. 15) specifically says black "corresponds with 'normality'." Bamber did recognize that black "non-ticked" is a simple (not sex-linked) recessive to tabby (wild-type coloration). It was given the symbol *a*, the generally used symbol for recessive black (nonagouti) in mammalian genetics. Tabby or tiger-striped is the descriptive term for the phenotype of wild cats (*Felis sp.*). Thus black and yellow (orange) are to be thought of as distinct mutant types, and independent. The combination of the two mutants, *a a* (nonagouti) with yellow, hemizygous or homozygous, has been shown to look the same as yellow alone, a good example of masking or epistasis (see Robinson³⁸, Searle⁴¹).

The textbook authors thus could have easily avoided the error by involving the word mutant in their presentations. The essential points they were trying to present were sex-linkage and patchy expression in the heterozygote. The facts could have been simply expressed thus: "The yellow or orange mutant coat-color type in cats is sex-linked. The modern symbol is *O* (Committee on standardized genetic nomenclature for cats, 1968)⁹. The heterozygous female, *O/+*, shows the tortoiseshell effect, a yellow (*O*) and non-yellow (*o*⁺) patchwork."

It may be thought that we are splitting hairs, making too much of a minor issue, and that the textbook authors were merely trying to present things simply. We contend, however, that here is a fundamental flaw—a general failure to identify "genes" as mutants by comparison with a standard type (e.g., normal or wild type). Most textbooks pay only lip-service to the utility of the + symbol. Notable exceptions were Altenburg's¹ and Sturtevant and Beadle's⁵⁰ books. The concept was not even considered in the compendium on teaching genetics by Darlington and Bradshaw¹¹, although it was called to attention by Hollander^{22,23} and Jaap and Hollander²⁵.

Tradition has nine lives, and in the lucrative and high-pressure world of text-book publication, a deviation (see Miller³³ 1985) may be unwelcome. But how can we claim that we teach genetics as science instead of dogma if "facts" are not challenged?

References

- ALTENBURG, E. Genetics. Henry Holt, N.Y. 1945. Second ed. 1957.
- AVERS, C. J. Genetics. Willard Grant Press, Boston. 1980.
- AYALA, F. J. and J. A. KIGER, JR. Modern Genetics. Benjamin-Cummings Publ. Co., Menlo Park, CA. 1980. Second ed. 1984.
- BAMBER, R. Genetics of domestic cats. *Bibliographia Genetica* 3:1-86. 1927.
- BATESON, W. Mendel's Principles of Heredity. 1909. 3rd ed. Univ. Press, Cambridge, England. 1913.
- BREWER, G. J. and C. F. SING. Genetics. Addison-Wesley, Reading, MA. 1983.
- BURNS, G. W. The Science of Genetics. Macmillan, N.Y. 1969. Fifth ed. 1983.
- COLIN, E. C. Elements of Genetics. Blakiston Co., Philadelphia. 1941. Second ed. 1946.
- COMMITTEE ON STANDARDIZED GENETIC NOMENCLATURE FOR CATS. Standardized genetic nomenclature for the domestic cat. *J. Hered.* 59:39-40. 1968.
- CROW, J. F. Genetics Notes. Burgess, Minneapolis. 1950. Seventh ed. 1976.
- DARLINGTON, C. D. and A. D. BRADSHAW, Eds. Teaching Genetics in School and University. Oliver & Boyd, Edinburgh. 1966.
- and K. MATHER. The Elements of Genetics. Geo. Allen & Unwin Ltd., London. 1949.
- DODSON, E. O. Genetics. W. B. Saunders Co., Philadelphia. 1956.
- DONCASTER, L. On sex-limited inheritance in cats. *J. Genet.* 3:11-23. 1913.
- ELSETH, G. D. and K. BAUMGARDNER. Genetics. Addison-Wesley, Reading, MA. 1984.
- FARNSWORTH, M. W. Genetics. Harper & Row, NY. 1978.
- GARDNER, E. J. Principles of Genetics. John Wiley, NY. 1960. Second ed. 1964. Seventh ed. with D. P. Snustad 1984.
- GOLDSCHMIDT, R. B. Understanding Heredity. John Wiley, NY. 1952.
- GOLDSTEIN, P. Genetics is Easy. Lantern Press, NY. 1947. Second ed. 1955.
- HENDRICK, P. W. Coat variants in cats. *J. Hered.* 76:127-131. 1985.
- HERSKOWITZ, I. H. Genetics. Little, Brown, & Co., Boston. 1962. Second ed. 1965.
- HOLLANDER, W. F. The ABC's of genetics. *J. Hered.* 44:211-212. 1953.
- . Epistasis and hypostasis. *J. Hered.* 46:222-225. 1955.
- HUTT, F. B. Animal Genetics. Ronald Press, NY. 1964. Second ed. with B. A. RASMUSEN. John Wiley, NY. 1982.
- JAAP, R. G. and W. F. HOLLANDER. Wild type as standard in poultry genetics. *Poultry Sci.* 33:94-100. 1954.
- JENKINS, J. B. Genetics. Houghton Mifflin, NY. Second ed. 1979.
- KERR, S. J. Mutant allele frequencies in rural Wisconsin cats. *J. Hered.* 75:203-206. 1984.
- KING, R. C. Genetics. Oxford Univ. Press, NY. 1962. Second ed. 1967.
- . A Dictionary of Genetics. Oxford Univ. Press, NY. 1968. Second ed. 1974.
- KLUG, W. S. and M. R. CUMMINGS. Concepts of Genetics. Charles E. Merrill Publ. Co., Columbus. 1983.
- LITTLE, C. C. On the occurrence of a sex-limited character in cats. *Science* 35:784. 1912.
- MERRELL, D. J. An Introduction to Genetics. W. W. Norton, NY. 1975.
- MILLER, W. J. Appropriate gene symbols in teaching genetics. *Proc. Iowa Acad. Sci.* 92:115-118. 1985.
- MORAN, C., C. B. GILLIES, and F. W. NICHOLAS. Fertile male tortoiseshell cats. *J. Hered.* 75:397-402. 1984.
- PLATE, L. Vererbungslehre. Verlag Wilhelm Engelmann, Leipzig 1913. Second ed. Verlag Gustav Fischer, Jena. 1933.
- PUNNETT, R. C. Mendelism. Third ed. Macmillan, NY. 1911.
- REDEI, G. P. Genetics. Macmillan, NY. 1982.
- ROBINSON, R. Genetics of the domestic cat. *Bibliographia Genetica* 18:273-355. 1959.
- . Genetics for Cat Breeders. Pergamon Press, NY. 1971. Second ed. 1977.
- . Fertile male tortoiseshell cats. *J. Hered.* 76:137-138. 1985.
- SEARLE, A. G. Comparative Genetics of Coat Colour in Mammals. Academic Press, London. 1968.
- SERRA, J. A. Modern Genetics. Academic Press, London. 1965.
- SINGLETON, W. R. Elementary Genetics. Van Nostrand, Princeton, NJ. 1962. Second ed. 1967.
- SINNOTT, E. W. and L. C. DUNN. Principles of Genetics. McGraw-Hill, NY. 1925. Fourth ed. with T. DOBZHANSKY. 1950. Fifth ed. 1958.
- SIRKS, M. J. Handboek der algemeene Erfelijkheid. Martinus Nijhoff, The Hague. 1922. Fifth ed. 1951. English ed., General Genetics. 1956.
- SNYDER, L. A., D. FREIFELDER, and D. L. HARTL. General Genetics. Jones & Bartlett, Boston. 1985.
- SNYDER, L. H. The Principles of Heredity. D. C. Heath, Boston. Fifth ed. with P. R. DAVID. 1957.
- SRB, A. M. and R. D. OWEN. General Genetics. W. H. Freeman, San Francisco. 1952. Second ed. with R. S. EDGAR. 1965.
- STRICKBERGER, M. W. Genetics. Macmillan, NY. 1968. Third ed. 1985.
- STURTEVANT, A. H. and G. W. BEADLE. An Introduction to Genetics. W. B. Saunders, Philadelphia. 1939.
- SUZUKI, D. T., A. J. F. GRIFFITHS, and R. C. LEWONTIN. Introduction to Genetic Analysis. W. H. Freeman, San Francisco. 1976. Second ed. 1981.
- TODD, N. B. and A. T. LLOYD. Mutant allele frequencies in domestic cats of Portugal and the Azores. *J. Hered.* 75:495-497. 1984.
- WAGNER, R. P., B. H. JUDD, B. G. SANDERS, and R. H. RICHARDSON. Introduction to Modern Genetics. John Wiley, NY. 1980.
- WALTER, H. E. Genetics. Macmillan, NY. 1913. Fourth ed. 1938.
- WHITE, E. G. Principles of Genetics. C. V. Mosby, St. Louis, MO. 1940.
- WHITTINGHILL, M. Human Genetics and its Foundations. Reinhold, NY. 1965.
- WINCHESTER, A. M. Genetics. Houghton Mifflin, Boston. 1951. Fourth ed. 1972.