

Cats and Commerce

Cats have had a long association with people but have rarely been intentionally bred for specific characteristics. The distribution of their mutants thus reflects certain human tastes and movements

by Neil B. Todd

At first cats would not seem to offer a likely clue to human history. Yet when one considers that the writing of adequate histories of human populations began scarcely 200 years ago, that writing itself dates back only about 6,000 years and that for many populations historical, linguistic and cultural records are inadequate or nonexistent, cats appear in a different light. They have been associated with human beings for a long time, but they have never had any economic significance and only rarely have they had much social significance. Genetically they, unlike other domesticated animals, have been left largely to themselves. The study of the population genetics of cats is therefore rewarding not only for what it reveals about the evolution of cats but also for what it suggests about the movements of human populations.

The study of population genetics has in general become a powerful tool for unraveling human history and prehistory and particularly for solving problems of the origin and dispersal of plants and animals. Each individual study, however, brings out limitations in both the organism being investigated and the approach made to the study. To obtain greater precision in the interpretation of complex events it is therefore desirable to study a number of species. Cats would qualify for this reason alone, but they have several advantages in addition to the ones I have already mentioned.

One advantage is that cats display visible polymorphisms, or variable traits, for which the genetic bases are reasonably well understood. Most of the polymorphisms relate to the color, pattern and texture of the fur and so can be diagnosed and recorded at a glance. Hence the accumulation of data is a relatively inexpensive procedure, unencumbered by sophisticated techniques and technologies.

Cats are cosmopolitan, thanks to the exploratory and commercial activity of human beings. The animals have been spread from their homelands in the Old World to every inhabited part of the

earth. They even persist in areas that people have abandoned. In addition to being ubiquitous cats are numerous. Most populations number at least in the hundreds, and many of them doubtless reach the millions. As a result the geneticist has both abundance and inherent genetic stability to work with.

Although further observations are required to assess certain complexities, most cat populations approximate what is known in genetics as the Hardy-Weinberg equilibrium. The expression means that the frequencies of various genetic factors can be stated in terms of theoretical mathematical distributions applying when it is assumed that populations are very large, randomly breeding and free from the complexities introduced by mutation, selection and migration. In the real world, of course, these criteria are never met. If they were, geneticists would have nothing to study. The apparent conformity of cat populations to the Hardy-Weinberg equilibrium does not mean that the influences of mutation, selection and migration are not important; rather, it means they take a relatively long time to bring about changes. Hence differences between populations can be ascribed to systematic forces rather than erratic ones. With cats one such force has been man, who in taking cats with him wherever he has gone has inadvertently conducted a series of experiments in population genetics that can now be evaluated.

The basic strategy in population genetics is the survey of a population. In practice the survey is usually a sampling. A sample can be gathered in a variety of ways, but the object always is to tabulate the frequency of phenotypes (observable characteristics of the organism) controlled by mutant alleles (variable genes). From seven to 10 such characteristics can be scored simultaneously in cat populations by simply looking at the cats.

The cats, of course, are only a transient packaging of genetic information. In the final analysis it is the gene pool

that is evolving. Therefore the geneticist is seeking not phenotype frequencies but mutant-allele frequencies, which are usually quite different from what is actually seen because of the ways in which each trait is inherited and interacts with other traits. A discussion of the mathematical manipulations whereby phenotype frequencies are translated into mutant-allele frequencies would be out of place here. The end result is the construction of what is known as a cline map, which shows the frequency with which certain mutant alleles appear in a given geographic area. The maps, then, become the relevant observation. Three such maps accompany this article; I shall return to them when I discuss some feline phenotypes.

Underlying any interpretation to be made from the cline maps and the data they reflect must be an appreciation that what is being studied is the complex of adaptations of an organism shifting from one ecological niche to another. The cat has moved, or is moving, from a wild and predatory life-style to a domesticated and subsidized one. It is evolving to a new niche, which is essentially the urban habitat. In the process it is experiencing a new set of interspecies and intraspecies relations.

What does this experience have to do with coat colors? In mammals there is a definite (but only rudimentarily understood) relation between pigmentation and endocrine chemistry. For example, the pigment melanin and the hormone adrenalin share a metabolic pathway, a common precursor being required for the synthesis of each. Studies of several kinds of animal have revealed that basic

THREE MUTANT CATS are portrayed in the illustration on the opposite page, together with the "wild," or nonmutant, type (a). The mutants, which embody traits controlled by certain alleles, or variable genes, are nonagouti (b), which is most commonly represented by the black cat; blotched tabby (c), and sex-linked orange (d). The color, pattern and texture of the fur provide a ready means of ascertaining the presence of the mutant alleles.

a



b



c



d



a



b



c



VARIANTS CONTROLLED BY THE SEX-LINKED-ORANGE ALLELE are represented by the tortoiseshell (a), calico (b) and marmalade (c) cats. Tortoiseshell and calico cats are usually female, since the orange mutation is located on the X, or female, chromosome. A female has two X chromosomes and so can simultaneously express both orange and nonorange traits.

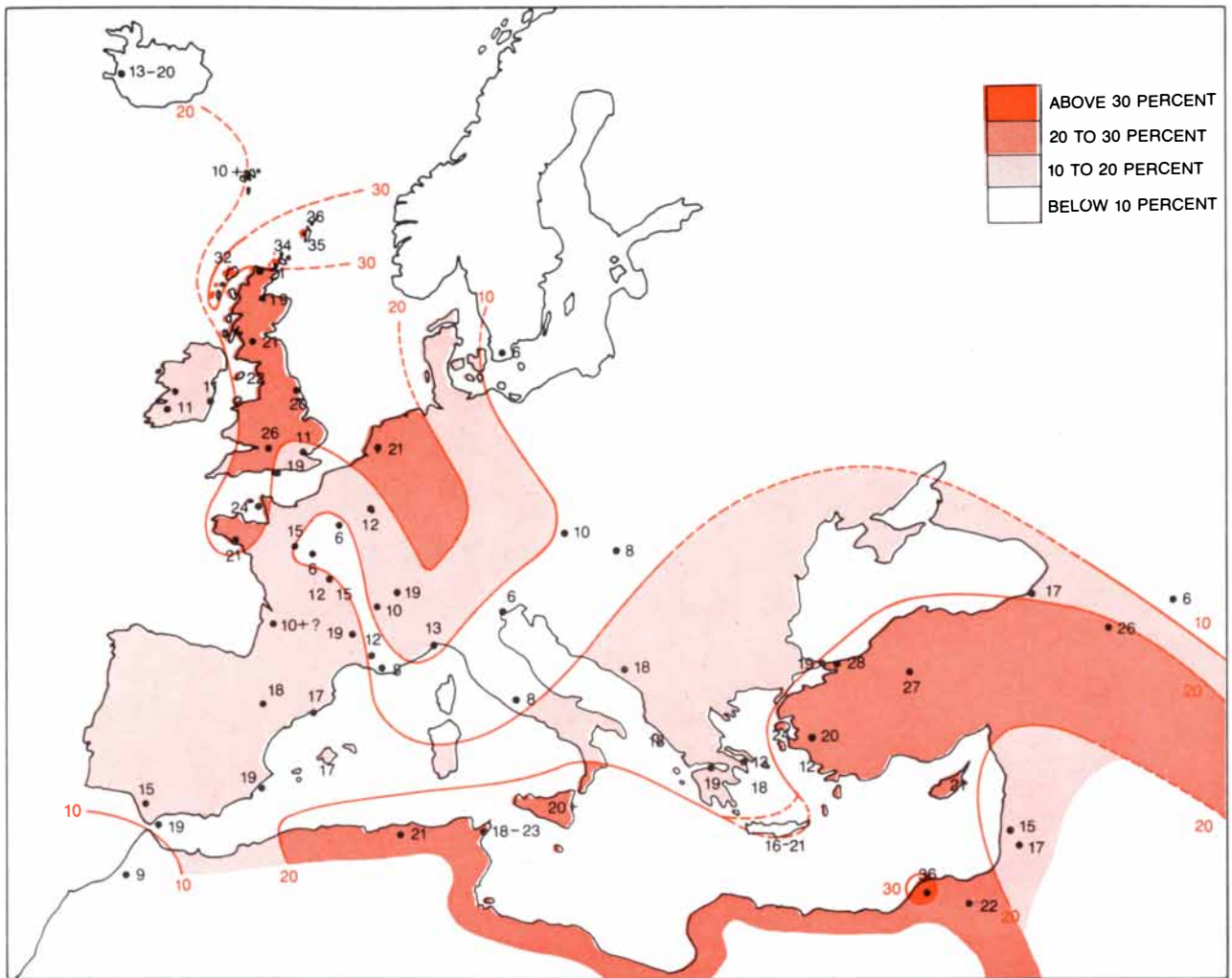
behavioral traits such as fear and aggression can be manipulated by simply crossing different coat-color mutants. Such effects have been documented for rats, mice, mink and foxes; if the effort were made, the same effect would almost certainly be revealed in cats and probably in all other mammals.

A piece of evidence here is that virtually every mutation in the cat shows a differential selective sensitivity to some feature or features along an urban-rural axis. For example, the genetic profiles of the cats of London and Paris show more similarities to each other than either profile does to that of the rural cats of Brittany. The selective forces responsible for these distinctions seem to be powerful; in one study the cats of urban and suburban Glasgow could be distinguished from one another. In a number of ways this spectrum of habitats is a spatial representation of the most important changes that have taken place in the living conditions of cats over the centuries. Recall that only the small towns and rural communities of today retain ecological features that were almost universal until a few hundred years ago. In ancient times a community of 10,000 inhabitants constituted a major urban complex. Only a few cities, such as Alexandria and Carthage, had populations of more than 100,000.

Since people and cats are inextricably associated in the process of domestication, it is necessary to look at some of the ways in which they do and do not interact. I have already noted that intentional human direction in modifying the gene frequencies of cats is largely negligible. There are, however, certain exceptions.

One of them might be termed novelty selection. This phenomenon derives from the human penchant for the odd and the curious or for the esteem of rarity. It may have had far-reaching ramifications in the history and development of all domesticated animals, but it seems most conspicuous today in the cat.

As background one should bear in mind that a new mutation, whatever its intrinsic adaptive value may be, is at a high risk of loss through the vagaries of chance. Geneticists refer to the process as genetic drift. In populations of cats one can observe that several mutant alleles stand at values that give their respective phenotypes a frequency of about 10 percent over large geographic areas or a maximum of 10 percent in scattered localities. The figure holds for mutant alleles that are inherited as dominant (controlling traits such as whiteness and polydactyly, referring to an excess of toes over the normal number), recessive (long hair and the Siamese pattern) or lethal (Manx taillessness), even though some of the traits are not beneficial to the animal.



CLINE MAP indicates the distribution of the sex-linked-orange allele in terms of percents. Such a map is made by sampling the cat population in a number of places and mathematically translating the observable traits of the sampled animals into mutant-allele frequencies.

The contour lines give percents in increments of 10, and more precise percentage figures are given for a number of cities. The clinal data suggest that the focus of the sex-linked-orange allele, that is, the location where the mutant first obtained a foothold, was in Asia Minor.

The explanation seems to be that when a phenotype reaches 10 percent, it is no longer perceived as being novel and is therefore regarded with indifference. If the phenotype's incidence begins to fall, however, it may be favored again. Hence a noteworthy type of selection, which could be called frequency-dependent selection, operates to facilitate the introduction and maintenance of genetic variation in populations. Presumably at the other end of the scale a highly advantageous mutation will be prevented from entirely displacing its alternative (going to fixation) by the same force. This unusual system may underlie the richness of genetic variability seen in domesticated animals, although in the more exploited species the variations are rapidly partitioned into breeds tailored for some particular human requirement. In cats, since the animals do not rank high in economic or social affairs, such variations simply

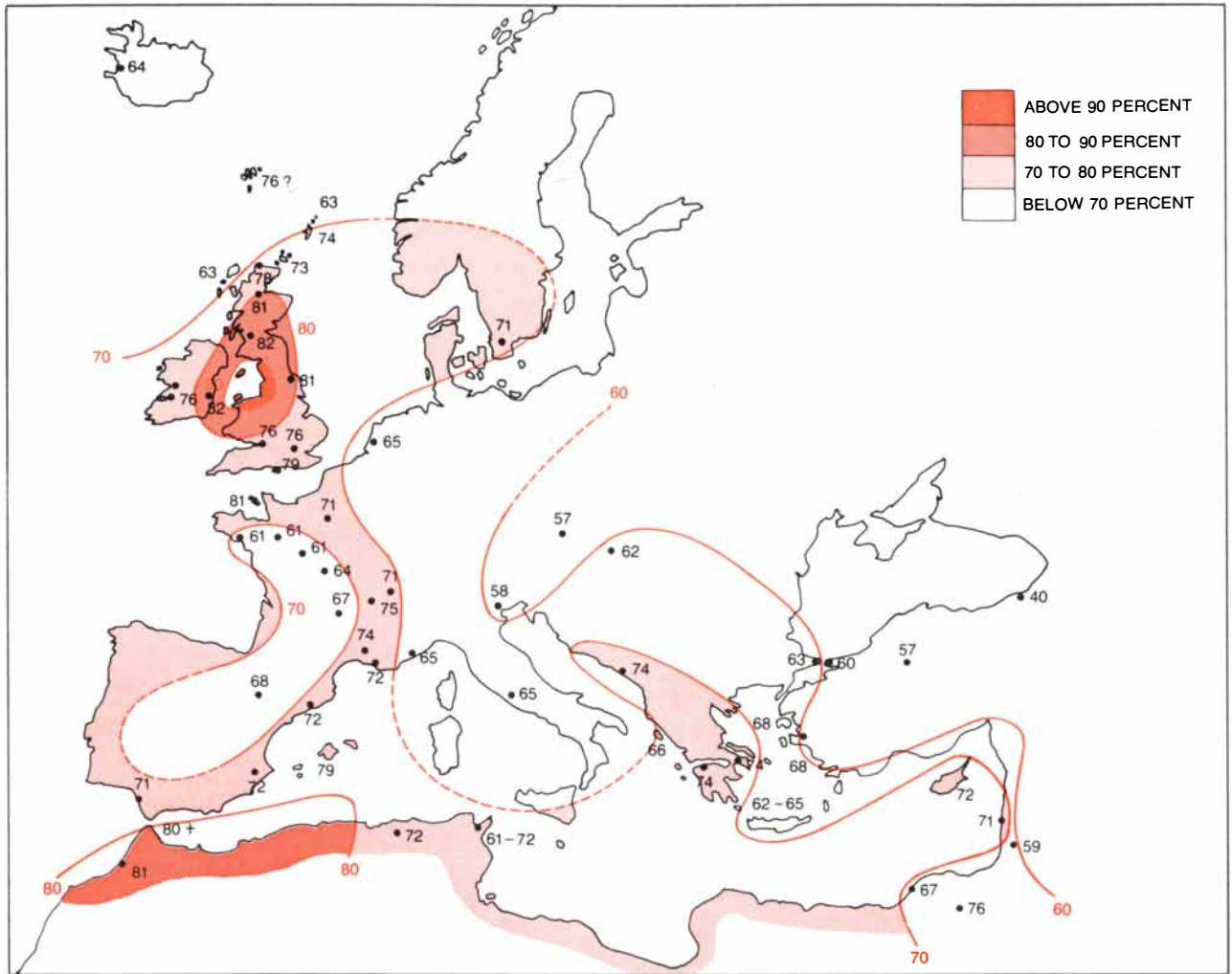
become dispersed throughout populations.

A second exception results from what can be called selective migration. Paradoxically, what are water barriers to most animals become veritable highways to cats. Most domestic animals have been transported over water, of course, but usually they go under strict control. Cats actually take up residence on ships and come and go at will (at the risk of being left in port). Apparently as soon as men had mastered the art of commercial navigation, cats became habitual members of the ship's company.

The choice of feline shipmates may do little more than extend novelty selection. On the other hand, it may promote further genetic change owing to circumstances that enable basic aesthetic (or other) preferences to become effective agents of selection. Whatever the reasons for the choice of cats, the effect in

maritime migrations may be particularly strong. The animals involved are often removed from the inertia implicit in being part of a large population and are transported to a smaller community. A human preference that would be swamped in a settled cat population can become quite evident in a migratory population.

Inevitably some mutations confer special advantages in certain circumstances. A familiar example involves the allele for darkness in moths; in normal circumstances it is deleterious, making the moth too conspicuous to birds, but in sooty industrial areas it makes the insect less conspicuous. When the normal background rate of mutation is coupled with novelty selection and migratory selection, the generation of variability is accelerated and the process of adaptation is facilitated. The mutant, preserved and secured, as it were, by special selection, now comes under the influ-



NONAGOUTI ALLELE is distributed as depicted in this cline map. Agouti, named for the South American rodent that exemplifies the condition, is a salt-and-pepper appearance caused by the fact that each hair of the fur has a band of reduced pigmentation below the tip.

The nonagouti mutation eliminates the band and brings about a more uniform pigmentation, which is most commonly black. The distribution suggests that a major focus of the mutation (some 2,500 years ago) was in the eastern Mediterranean, probably Greece or Phoenicia.

ence of natural selection, in the sense that its fate is no longer linked directly to the idiosyncrasies of man. The mutation may impart some intrinsic superiority, such as resistance to disease or a broader tolerance in nutritional requirements, or it may modulate behavior in such a way as to reduce friction between species and within the species. Whatever the contribution, new forces come into play according to the nature of the genetic difference.

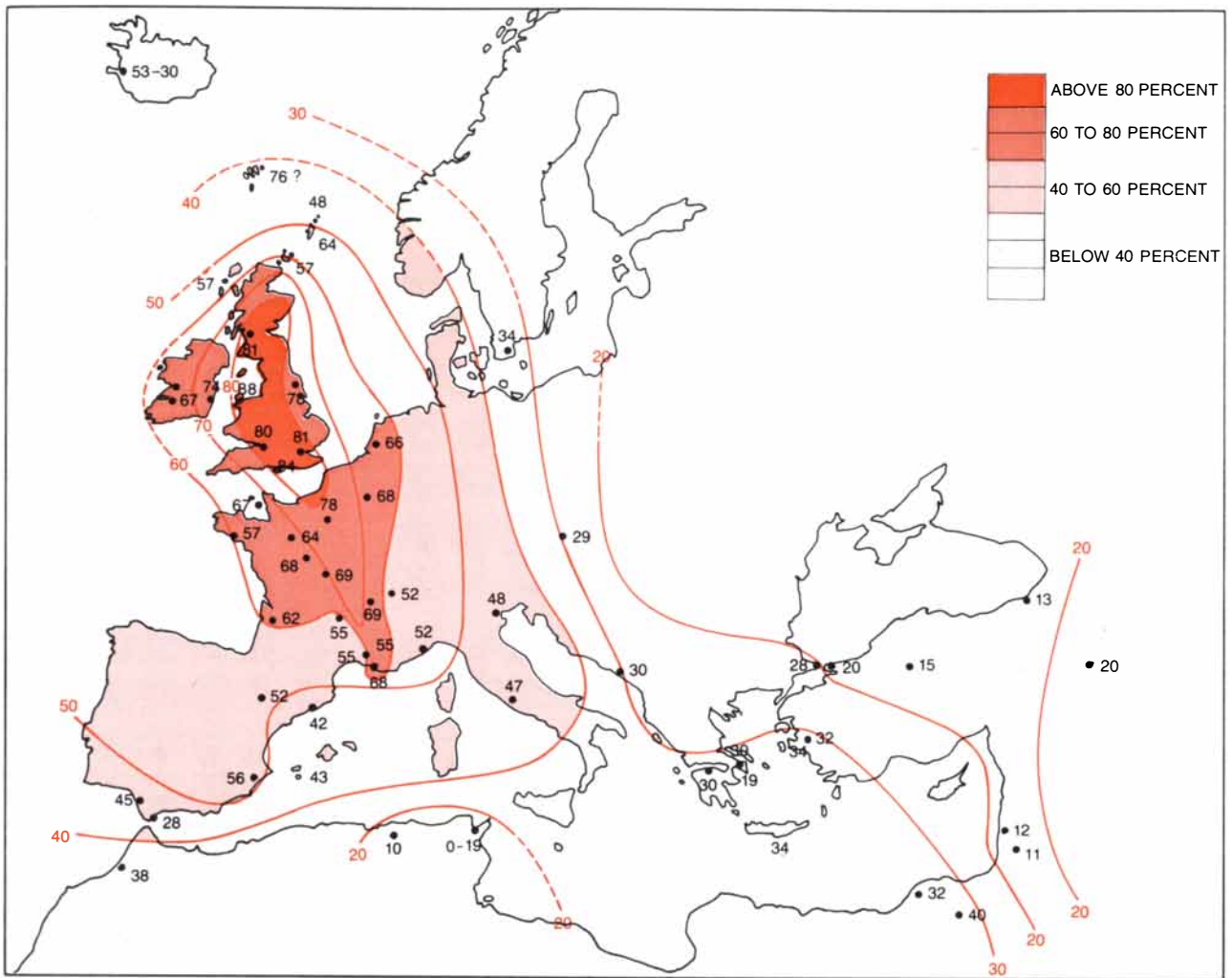
In some cases mutants are most successful in the heterozygous state. (An organism receives half of its genes from the mother and half from the father. If both of the two gametes, or sex cells, that fuse during fertilization carry the same gene for a certain trait, such as coat color, the offspring is homozygous. If they carry different genes for the trait, the offspring is heterozygous.) Heterozygosity may impart a "hybrid vigor," in which case the mutants will reach an equilibrium according to the relative fit-

ness of the two homozygous alternatives. Other factors may be most advantageous only in one of the homozygous combinations. Then the mutants rise toward fixation at a rate that depends on the relative adaptive values of the alternative genotypes. Finally, a mutation may confer no inherent advantage, although because of its novelty it is preserved and dispersed at low levels.

Among the four cat genotypes I shall discuss below, the evidence suggests that one, sex-linked orange, imparts a heterozygous advantage; that another, nonagouti (usually black), manifests features of heterozygous and homozygous advantage, depending on the circumstances; that a third, blotched tabby, is so powerfully favored in the homozygous state that it is driving inexorably to displace its alternative allele, the wild type, and that the fourth, polydactyly, persists as a curiosity. My assumptions about selective forces are based partly on the clinal distributions

and partly on other evidence and theoretical considerations. No unequivocal proofs have yet been produced; the following discussion therefore serves mainly to describe some of the hypotheses that are being put forward as guidelines for further study.

It is worth noting explicitly the underlying assumption that the present heterogeneous patterns of the four mutants (as well as of other mutants) have arisen from an ancestral population that was relatively uniform and homogeneous. Thus a fundamental influence in the distribution of any mutant is the time and place of "origin," by which is meant the time and the site in which the mutant initially secured a foothold. Such a point becomes the focus for further dispersal, whatever the mutant's precise geographic point of origin may have been. I therefore employ the term focus to cover the situation, with the understanding that the literal place of origin may or may not be coincidental.



BLOTCHED-TABBY ALLELE exhibits this distribution. The map can be read to suggest two foci for the allele, one (the more prominent) in Britain and one in northeastern Iran. The westward flow of the mutant from the focus in Iran seems to be merging in Asia Minor

with the eastward flow from the focus in Europe. The hypothesis of Britain as a focus of the allele is supported by the numbers of cats bearing the allele in New England, Canada, Australia and New Zealand, all of which were colonized over some 300 years from Britain.

Sex-linked orange is a mutant responsible for a variety of well-known phenotypes, depending on the sex and the genotype of the individual carrying the gene and on certain interactions with other mutants. The most familiar examples are the cats commonly called marmalade, tortoiseshell and calico. Tortoiseshell and calico cats are almost always female, since the phenotype depends on heterozygosity. (The orange mutation is located on the female, or *X*, chromosome. Since a female has two such chromosomes, she can carry and simultaneously express both orange and nonorange. Males normally have only one *X* chromosome, the other one being *Y*, and so a male can express orange or nonorange but not both at once.) This is a fascinating story in itself, but in the present context the relevant point is that the frequency of the sex-linked-orange allele is not known to rise above 36 percent anywhere in the world; 25 percent is closer to the usual level. This observa-

tion leads to the tentative conclusion that the basic equilibrium is at about 25 percent, which is a likely level to obtain in cases of heterozygous advantage. Hence the most parsimonious interpretation of the clinal distribution of the sex-linked-orange allele is that where the percentage is lower than 25 an equilibrium has not yet been struck, and where it is higher the equilibrium has been disturbed.

The cline map showing the distribution of the sex-linked-orange allele presents an extraordinary pattern: an irregular central area with frequencies distinctly lower than those found outside the core. The full explanation for this pattern is elusive, but one of the geographic features—the corridor through France, linking London and the Mediterranean—is explainable. The valleys of the Seine and the Rhône, augmented in recent times by an elaborate barge-canal system, have long been a highly developed maritime route employed as an

alternative to the transport of goods by way of the Strait of Gibraltar.

This inland conduit is a constant feature in the distribution of three of the four mutants under consideration. It has clearly served to promote the dispersal of nonagouti, blotched-tabby and other mutants but seems to have had an opposite influence on sex-linked orange. The low values of the mutant in parts of the core, Rome and Marseilles in particular and perhaps London too, are attributable to the long, continuous presence of large populations of cats. When sex-linked orange reached those areas, it would have represented only a small fraction of all the alleles present. Hence the low frequency of the mutant in the corridor reflects little more than the reduced opportunity for the recruitment of sex-linked-orange cats as migrants. The long stability of the cat population in turn probably reflects the centuries of Roman hegemony in the region.

Can the focus of the mutant be de-

duced from the clinal distribution? The relatively high frequency of sex-linked orange along the northern coast of Africa, in the Balearic Islands and along the Mediterranean coast of Spain suggests a migration from the east over water. Asia Minor therefore emerges as a potential focus, since the frequencies there are comparatively uniform and presumably at an equilibrium over a large area. With certain exceptions the levels drop off in every direction.

What, then, would account for the high frequency of the mutant in the islands off the northern and western coasts of Scotland and to a lesser extent in rural Iceland, the Faroe Islands and the Isle of Man? The frequency of dominant white is also higher there than almost anywhere else. Could it be that 1,000 years after they were introduced to these last outposts of European civilization cats still reflect what may have been aesthetic preferences of the Vikings?

The only other place where this combination of orange and dominant-white frequencies is known to occur is the remote district of Van in eastern Turkey. It is noteworthy that dominant-white

cats, although they may be pleasing to the eye, are basically a disadvantaged genotype. They suffer from reduced viability, and the ones that survive are often afflicted with defects of sight and hearing and are susceptible to certain kinds of skin cancer. Wherever their numbers are high, the hand of man can be inferred. The evidence suggests that the Vikings selectively transported this profile of sex-linked orange and dominant white from their contacts on the Black Sea and planted it in the North Atlantic.

Turning to the mutant nonagouti, the most common manifestation of which is the black cat, certain broad features are worth mentioning. Agouti (so named because the agouti, a South American rodent, exemplifies the suite of characteristics well) is a basic mammalian condition. The agouti phenotype is due primarily to the distribution of melanin in the hair shaft in such a way as to produce a band of reduced pigmentation below the tip of the hair. The result is a salt-and-pepper, or brindle, pattern. A simple recessive mutation, nonagouti, eliminates this band and so gives rise to

a hair that is more or less uniformly pigmented along its length.

Most mammals are agouti, but most domesticated mammals are nonagouti. The cat is something of an exception in that everywhere it shows a sharp dimorphism for the two alternative states. Some 150 surveys have revealed that nonagouti stands at above 50 percent. The finding is strong circumstantial evidence that a basic equilibrium exists at this level and that it is probably determined by heterozygous advantage.

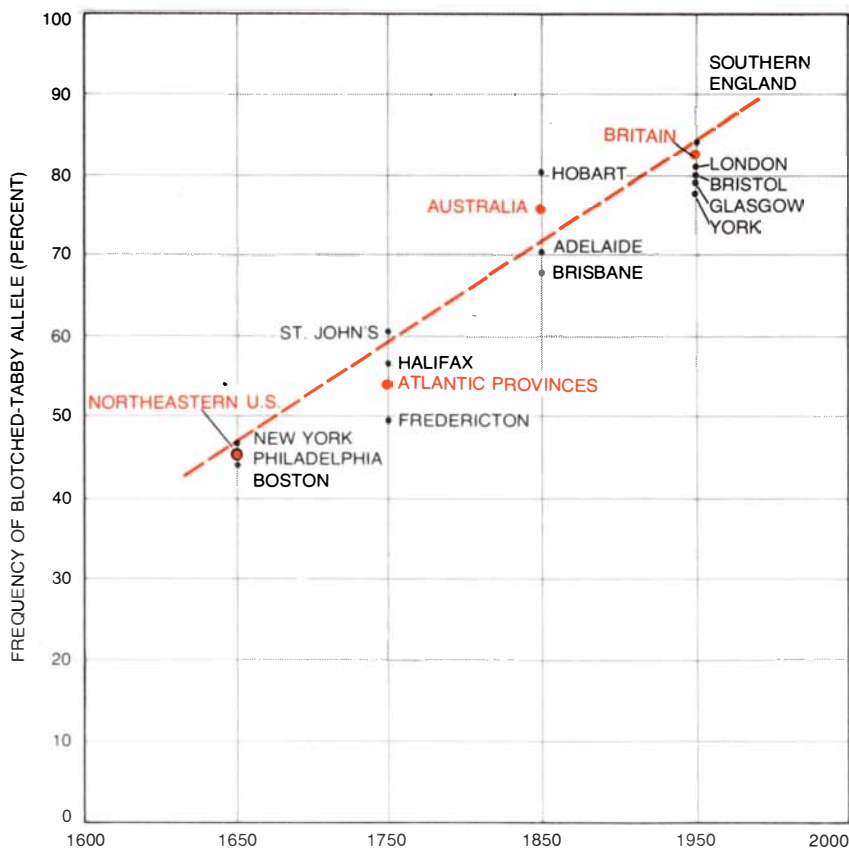
Can the hand of man be seen in the distribution of nonagouti cats? The highest frequencies of the mutant are found in Britain and in parts of northwest Africa. Slightly lower frequencies predominate along the narrow corridor through central France and throughout most of the Mediterranean; Rome and Venice are conspicuous exceptions.

The evidence is strong that the nonagouti mutant is favored by the urban habitat. If the evidence is construed to mean that the mutant is instrumental in fostering the cat-human affiliation, some sensible interpretations can be made. The high values in Britain stem from the high degree of affiliation implicit in selective migration, reinforced by intensive urbanization. The significance of the corridor through France is again that it had a principal role in the movement of commerce.

Although the British and northwest African areas are undoubtedly serving now as major foci, the high frequencies of the mutant there were created initially by the sequential intensification of frequencies through selective migration. In other words, each time people embarked to expand their sphere of civilized activity they took along an increasingly concentrated sample of nonagouti cats. Was the first step in this process, at least in the classical Mediterranean, taken by Greeks and Phoenicians in their colonization of Massilia and Carthage? Was a second step taken by Carthaginians when they founded communities in the Balearics, Algeciras, Tangier and Rabat?

Blotched tabby displays a close approach to the ideal dissemination of a mutant. The pattern, taken at face value, suggests a British focus (and in this instance probably a British origin), penetration through France and a rapid spread eastward across the Mediterranean. An eastern focus has recently been identified in or adjacent to northeast Iran. The westward flow from this focus seems to be merging on the Anatolian plateau of Asia Minor with the eastward flow from Europe.

The selective advantage shown by the blotched-tabby mutant is a mystery. The type is clearly spreading like an epidemic that will apparently engulf all cat populations. Even among the feral cats of Tasmania the mutant demonstrates



TIME AND FREQUENCY of blotched-tabby allele are plotted according to a system in which the date assigned to each community (black dots) and region (colored dots) is the approximate year in which the place was colonized by Britain and the present frequency of the allele in each place approximates the frequency it had in the British cat population at the time of colonization. The line representing the average predicts closely the present frequency of the allele in Britain (upper right), supporting the inference from the cline map pertaining to blotched tabby that the allele has been rising rapidly in Britain and diffusing steadily into surrounding areas.

superiority to the alternative (the wild type) in the face of a selection pressure that is rapidly reducing most of the other mutants to low levels.

Since the blotched-tabby allele presumably arose rather recently, and since it shows such a powerful impetus to spread, few clues for tracing its history can be found in the Old World clines. Data from the New World, Australia and elsewhere supplement the picture of Britain as a focus.

Beginning in the 17th century British cats were exported to lands that had no indigenous cats. New England, Canada, Australia and New Zealand were all recipients, at different times, of British propagules. If the premise is accepted that each of these populations was based on a representative sample of British cats drawn off over a period of 300 years, an interesting relation appears between the frequency of certain alleles and the time of sampling. Blotched tabby is the key to this analysis, since it shows a dramatic correlation.

Suppose various places are assigned dates according to the time of initial settlement, and the present genetic profiles of cats in those areas are taken to approximate those of the original cat population; it is then possible to plot time against frequency. This exercise reveals a trend, established in the first 200 years, that predicts the present frequency of blotched tabby in Britain with remarkable accuracy. The finding reinforces the appraisal, based on the cline map of the Old World, that the blotched-tabby allele has been rising rapidly in Britain and diffusing into surrounding populations. Comparable analyses of the exploration and colonization by the Dutch, the French, the Portuguese and the Spanish would probably yield similar pictures.

My final example concerns a mutation resulting in extra digits. (Polydactyly, meaning many digits, is not really an accurate term.) Cats with this condition are common in New England, New Brunswick and Nova Scotia, where they may constitute more than 10 percent of all individuals. Elsewhere, however, except for isolated pockets, they are rare.

The evidence suggests a New England origin, or at least a New England focus, for the dispersal of such cats, doubtless on the basis of novelty. The strong likelihood that the cats must have been present in, say, Boston by the middle of the 18th century is supported by their equal abundance today in Halifax. That city was not founded until the middle of the 18th century, and then it was at first a center of commercial activity involving New England and later a refuge for thousands of Loyalists fleeing the American rebellion. It would seem that the people who traveled to Halifax transported more than goods, services and political persuasions. They also took their polydactyl cats.

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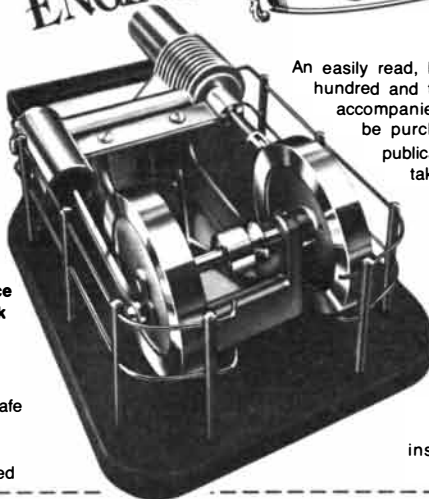
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