

A Short Natural History of the Cat and Its Relationship with Humans

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OUTLINE

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More than 71.1 million homes in the United States, approximately 59.5%, contain pets, and many owners have more than one pet.³ According to the 2007-2008 National Pet Owners Survey, 38.4 million households in the United States, 54% of pet owners, own a cat. There are 88.3 million cats, compared with 74.8 million dogs, implying roughly 13.5 million more cats than dogs in U.S. households. A survey conducted by the American Veterinary Medical Association (AVMA) reported a 12.4% increase in pet ownership from 2001, when 61.1 million households contained a pet, to 2006, when 68.7 million households were estimated to include a pet.⁴ Although the estimate of pet owners is slightly different in the two surveys, the trends are the same: Cats are increasing in popularity as companion animals in the United States. In the United Kingdom, households with dogs appear to be more common than those with cats; however, the number of owned cats and dogs is about the same.⁴⁸ Worldwide, domestic cats are clearly gaining in popularity, perhaps being more conducive pets to the modern lifestyle, and, as the cat's status upgrades from mere pet to family member, cat health care has become a common family value.

In tandem with human migrations, cats have traveled around the world, generally to work as vermin control on boats and farms; thus their population management has generally been unrestricted. The cat's co-migrations with humans have resulted in large feral cat populations in both highly populated cities and remote islands that have or previously had human occupation.⁵⁰ Because cats, as non-native species, severely threaten native

wildlife species,²⁹ their management is a matter of significant debate, even though the resulting feral populations are due to human negligence. Many cats from the feral populations are captured and transferred to shelters. People are increasingly concerned about the welfare of cats in shelters, and shelter managers must balance kill versus no-kill strategies to ensure adequate population control.²⁹

Currently, cats continue to travel the world but more commonly as our valued companions, thus contributing less to feral populations. Although migrant cats confuse the identity of a population's original genetic composition, the origins of the domestic cat can be traced to the dawn of human civilization by following human migrations back through time and sampling the random-bred, remote, and feral cat populations of the world.

DOMESTIC CAT ORIGINS

The domestic cat, *Felis catus*,^{24,37} is one of 38 species in the cat family *Felidae*, being a member of the *Felis* lineage.⁵¹ The *Felis* lineage is composed of three small African felids and four small felids that may be the progenitors of the domestic cat, including *Felis lybica* (African wildcat), *Felis silvestris* (European wildcat), *Felis ornata* (Asian wildcat), and *Felis bieti* (Chinese desert cat).^{27,31} The domestic cat and the wildcat species can interbreed, producing fertile hybrids²⁵; thus their demarcation as subspecies and even distinct species can be disputed. Because the common housecat is a

domesticated derivative, the term *Felis catus* has been re-adopted and does not clearly denote the genetic relationship to the progenitor wildcats or their subspecies.²⁴ The relationship of the African, European, and two Asian wildcats is somewhat controversial; currently, 21 subspecies are defined within these groupings.³³ Other than the South African subspecies of African wildcat, *Felis lybica cafra*, most species of wildcat and their associated subspecies may be the progenitors of domestic cat populations.^{21,39} *Felis lybica* having the most scientific support. The African wildcat definitely influenced the origins of the domestic cat²¹; however, detailed examinations of other wildcat species and subspecies have not been possible because of poor access to appropriate samples. For two wildcat subspecies, European and Scottish wildcats, introgressions with domestic cats may be an ongoing process,^{7,55-57} threatening the existence of “pure” wildcat populations in Europe and the United Kingdom. Conservation efforts to protect the wildcat populations in Scotland, Italy, the Iberian Peninsula, and other regions fight the encroachment of domestic cats—household pets that may be returning to their feral states, obscuring and perhaps reversing the domestication process.^{43,54}

Domestic cats likely participated actively in their own domestication; humans and felines developed a symbiotic, commensal, mutual tolerance. Several independent sites of early civilizations are known to have developed between 8000 and 3000 BCE, including the Huang He River region of China, the Indus Valley in Pakistan, and the Fertile Crescent region, which extends from Iraq, into Turkey, south along the Levant region of the Mediterranean coast, and, arguably, into the Nile Valley of Egypt.⁸ As humans made the transition from hunter-gatherers to the more sedentary lifestyle of the farmer and permanent settlements subsequently developed, villages produced refuse piles and grain stores, attracting mice and rats,¹¹ a primary prey species for the small wildcat. To obtain these easy meals, bold wildcats perhaps began to tolerate humans, and humans accepted the cat because of its utility in vermin control.

Arguably, the domestication of the cat can be considered incomplete and in flux, because abandoned cats and feral populations can quickly adapt to a wildcat lifestyle.^{19,20} The cat has behavioral and social attributes recalcitrant to domestication, such as being highly agile and a mainly solitary species; these very traits may be part of the reason that many humans find cats so fascinating and endearing. A combination of self-selection by the cat and selection by humans has led to a variety of aesthetically pleasing coat colors and traits specific to domesticated cats and behaviors that are conducive to companionship. A comprehensive review of coat color frequencies,^{40,61} such as those performed in Great Britain,²⁶ have corroborated cat migrations and human selection preferences by indicating clines of higher and

lower coat color frequencies across the world. These clines suggest some degree of controlled breeding or selection by humans, which probably began with the cat seeking human affection and companionship in the Fertile Crescent region and later became more systematic with the first controlled cat breeding programs, possibly in Egypt.⁴⁴

DOMESTIC CAT BREEDS

The creation of cat breeds has been a significantly different process than breed development in other companion animal and agricultural species.^{12,63} These nuances are important for an understanding of the appropriate genetic tools, resources, and techniques that will be the most beneficial and efficient for cat genetic research and health programs (see Chapter 43). Random-bred and feral cats represent the overwhelming majority of cats throughout the world, not fancy cat breed populations,³ although most genetic studies have focused on cat breeds to date. Considering the worldwide distribution of cats, the United States likely has the highest proportion of pedigreed cats. However, the proportion of pedigreed versus random-bred cats is still fairly low; only 10% to 15% of feline patients at the University of California, Davis Veterinary Medicine Teaching Hospital is represented by pedigreed cats.⁴¹ A general understanding of cat breed development and a more in-depth understanding of a limited number of foundation cat breeds will help the veterinarian predict health care problems on the basis of each patient’s genetic background. A knowledge of cat breed relationships also helps the veterinarian prioritize differentials for health care management.

Some of the earliest descriptions of different “types” of cats were documented in Siam (now known as Thailand) by monks during the Ayutthaya period (1350-1767).⁶² Korats, Burmese, and Siamese were clearly defined according to their coat colors. These same colorations define the same cat breeds today. The naturalist Georges-Louis Leclerc (Comte de Buffon) described races of domestic cats, identifying some of the current breeds, such as the Angora and the Chartreux, on the basis of coat colorations and fur length.³⁶ Early taxonomists used the coat variants to define domestic cats according to their different variants and subspecies.^{37,52,53} The aesthetic value of the coat color and type variants led to competitive showing and breeding. The first documented cat show that judged cats on their aesthetic value occurred in London, England, at the Crystal Palace in 1871.¹ This competition presented only a handful of breeds, including the British, Persian, Abyssinian, Angora, and Siamese. Thus, these early documented cat breeds likely represented genetically distinct populations insofar as strict breeding programs were not established at the time.

Within a few years, cat shows began taking place in the United States, and the homegrown Maine Coon cat was added as a specific breed. The Maine Coon developed from western European random-bred cats that had traveled to the New World with the pilgrims and colonial settlers. By the early 1900s, several cat fancy registries were established and stricter breeding practices were developed. In contrast, a wealth of dog breeds were well established by the twentieth century, having been in development for several hundreds of years.^{23,64} A variety of cattle¹⁴ and horse¹² breeds also existed, domesticated from various regional wild populations of the world. Several modern encyclopedic volumes pertaining to the domestic cat list approximately 50 to 80 cat breeds worldwide.^{46,47} However, a majority of breeds were developed in the past 50 years, and many listed breeds did not develop into viable populations; some no longer exist, in fact.

Another major difference between cats and other domesticated species lies in the selection process for cat breeds. Cats were originally, and continue to be, selected for aesthetic traits, such as coat colors and fur types, which are mainly single-gene traits. Cats performed their required function, vermin control, naturally. Dog breeds, however, have been selected for morphologies that support diverse functions and behaviors.⁶³ The breeds of agricultural species are selected for meat and milk quality and quantity.¹³ These behavioral and production traits involve complex interactions among many genes, which suggests that more selection has been applied to the genome of dogs, cattle, pigs, and chickens than to the genome of the domestic cat. Less selection likely results in more genetic diversity for cats, which may mean comparatively fewer health problems for cats than for other species.

However, significant distinctions are now apparent among the structural morphologies of current cat breeds.

On one end of the spectrum is the cobby and robust body of the Persian, which has extreme brachycephalia; on the other extreme is the slender and fine body of the Siamese, which has extreme dolichocephalia. The severity of these extremes, particularly in the facial structure, has led to certain feline health problems and resultant criticism^{34,59} for the cat fancy. A greater emphasis on selection, drawing on more complex genetic interactions, may soon lead to more health concerns.

Today's most pertinent cat breeds and their genetic relationships are listed in [Table 42-1](#). Most worldwide cat fancy associations, such as the Cat Fanciers' Association (CFA),^{16,17} The International Cat Association (TICA),⁶⁰ the Governing Council of the Cat Fancy (GCCF),² and the Fédération Internationale Féline (FIFe),²² recognize approximately 35 to 41 cat breeds, although only a few breeds overwhelmingly dominate the census of the registries. Persian cats and related breeds (e.g., Exotics, a shorthaired Persian variety) are among the most popular cat breeds worldwide and represent an overwhelming majority of pedigreed cats. Although not all cats produced by breeders are registered, perhaps only 20% to 30%, the CFA, one of the largest cat registries worldwide, generally registers approximately 40,000 pedigreed cats annually.¹⁸ Approximately 16,000 to 20,000 are Persians, and approximately 3000 are Exotics; thus the Persian group of cats represents more than 50% of the cat fancy population. Common breeds that generally have at least 1000 annual registrants are Abyssinians, Maine Coons, and Siamese. Other popular breeds include the Birman and Burmese, which are more prevalent in other areas, such as the United Kingdom. Most of these popular breeds also represent the oldest and most established cat breeds worldwide. However, because of different breeding standards in different registries and population substructuring, not all cats identified as the same breed are genetically alike. Disease frequencies may be different

TABLE 42-1 Domestic Cat Breeds of the World: Their Origins and Relationships

Breed	Place Founded	Breed (Family) Grouping*
Abyssinian	Founder—India?	Somali
American Bobtail	Mutation	United States—random breds
American Curl	Mutation	United States—random breds
American Shorthair	Founder—United States	American Wirehair
American Wirehair	Mutation	American Shorthair
Australian Mist	Hybrid	Burmese derived
Balinese	Variant	Colorpoint, Havana Brown, Javanese, Oriental, Siamese
Bengal	Species hybrid	Leopard cat × Egyptian Mau and Abyssinian
Birman	Founder—Southeast Asia	
Bombay	Variant	Burmese, Singapura, Tonkinese
British Shorthair	Founder—Europe	Scottish Fold

TABLE 42-1 Domestic Cat Breeds of the World: Their Origins and Relationships—cont'd

Breed	Place Founded	Breed (Family) Grouping*
Burmese	Founder—Southeast Asia	Bombay, Singapura, Tonkinese
Burmilla	Hybrid	Burmese, Persian
Chartreux	Founder—Europe	
Colorpoint Shorthair	Variant	Balinese, Havana Brown, Javanese, Oriental, Siamese
Cornish Rex	Mutation	United Kingdom—random breds
Devon Rex	Mutation	United Kingdom—random breds, Sphynx
Egyptian Mau	Founder—Mediterranean	
European	Founder—Europe	
Exotic	Variant	Persian
Havana Brown	Variant	Balinese, Colorpoint, Javanese, Oriental, Siamese
Japanese Bobtail	Founder	
Javanese	Variant	Balinese, Colorpoint, Havana Brown, Oriental, Siamese
Korat	Founder—Southeast Asia	
Kurilian Bobtail	Mutation	Eastern Russia, Kuril Islands
LaPerm	Mutation	United States—random breds
Maine Coon	Founder—United States	
Manx	Mutation	United Kingdom—random breds
Munchkin	Mutation	United States—random breds
Norwegian Forest	Founder—Europe	
Ocicat	Crossbred	Siamese × Abyssinian
Oriental	Variant	Balinese, Colorpoint, Havana Brown, Javanese, Siamese
Persian	Founder—Europe	Exotic
Peterbald	Mutation	Russian—random breds, Don Sphynx
Pixie-bob	Founder—United States	United States—random breds
Ragdoll	Founder—United States	United States—random breds
Russian Blue	Founder—Europe	
Savannah	Species hybrid	Serval × domestic
Scottish Fold	Mutation	United Kingdom—random breds, British SH, Persian
Selkirk Rex	Mutation	United States—random breds, Persian
Siamese	Founder—Southeast Asia	Balinese, Havana Brown, Javanese, Colorpoint, Oriental
Siberian	Founder—Europe	Russian—random breds
Singapura	Variant	Bombay, Burmese, Tonkinese
Sokoke	Founder—Africa	African—random breds
Somali	Variant	Abyssinian
Sphynx	Mutation	Devon Rex
Tonkinese	Variant	Bombay, Burmese, Singapura
Turkish Angora	Founder—Mediterranean	
Turkish Van	Founder—Mediterranean	

*Modified from genetic studies based on 29 tetranucleotide short tandem repeat markers,⁴⁵ 39 dinucleotide short tandem repeat markers,³⁹ and unpublished data (Lyons).

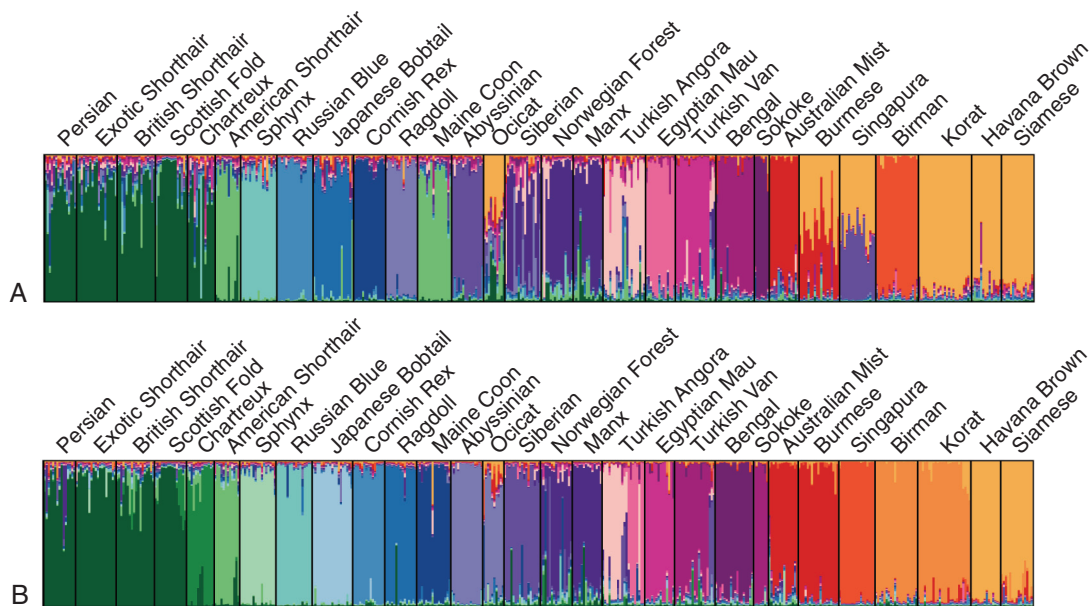


FIGURE 42-1 Population structuring of domestic cat breeds. The colors correspond to predicted genetic clusters. Each column represents an individual cat. **A**, Breed clustering defined by single nucleotide polymorphisms (SNPs). The slower mutation rate of SNPs resolves older breed relationships. There are 29 cat breeds that form only 17 distinct populations. Asian breeds, such as Burmese, Singapura, Birman, and Korat, are genetically distinct, but Korat, Havana Brown, and Siamese cluster. **B**, Breed clustering defined by short-tandem repeat, microsatellite markers (STRs). The faster mutation rate of STRs resolves more recent breed relationships. There are 29 cat breeds that form 21 distinct populations. Havana Browns and Siamese, and Burmese and Singapura are not genetically differentiated. Persian, Exotic Shorthair, British Shorthair, and Scottish Fold cannot be clearly defined. The Ocicat and Abyssinian relationship cannot be separated, nor can the Burmese and the Australian Mist.

for breeds in different parts of the world. For example, polycystic kidney disease has been shown to have about the same prevalence in Persian cats around the world,^{5,6,10,15} but hypokalemia in the Burmese is more limited to cats in the United Kingdom and Australia^{9,35} and not found in populations in the United States. Some lines of Burmese in the United States segregate for a craniofacial defect, which is not commonly found in Burmese cats outside the United States.⁴⁹ The breed substructuring may be partially due to rabies control measures that reduce migration of cats among countries, but it is also likely that the known health concerns in the breeds have led to strong restrictions of imports and exports of fancy-breed cats.

A more recently developed cat breed, the Bengal,³⁰ which is a hybrid between the Asian Leopard cat, *Prionailurus bengalensis*, and the domestic cat, has gained significant popularity throughout the world, even though some registries currently do not recognize the breed. The Bengal exhibits remarkable colorations and tabby patterns, but their temperament is generally a bit more fractious than that of other breeds. Several other hybrid breeds exist,⁶⁰ including crosses with Servals (*Felis serval*), known as Savannahs, and Jungle cats (*Felis chaus*), known as Chaussies. Because of limited wildcat founders, the hybrid cats may have decreased genetic variation. These hybrid cats may also have allelic incompatibilities for a given gene; the genes between the two

species, leopard cat and domestic cat, have millions of years of evolutionary divergence, which allows differences at the DNA sequence level of a gene. Hence an accumulation of different genetic variants that are functional within the species, but nonfunctional across the felid species, are likely present in some Bengal cats. Thus hybrid cat breeds may have unexpected health problems and infertility, creating a challenge for both genetic studies and primary health care.

Many modern cat breeds derived from an older “foundation” breed, thereby forming breed families or groups (see Table 42-1). Approximately 22 breeds can be considered foundation or “natural” breeds. Genetic studies have also shown that the foundation breeds have either significantly different genetic pools or sufficient selection and inbreeding that created significant genetic distinction (Figure 42-1). Cat breeds derived from the foundation breeds are often based on single gene variants, such as longhaired and shorthaired varieties, or even a hairless variety, as found in the Devon Rex and Sphynx grouping. Color variants also tend to demarcate breeds, such as the “pointed” variety of the Persian, known as the Himalayan by many cat enthusiasts and as a separate breed by some associations, such as TICA.⁶⁰ These derived breeds are not genetically significantly different and therefore share health concerns. Selkirk Rex, American Shorthair, and British Shorthair all use Persians to help define their structure; thus these breeds

also suffer from polycystic kidney disease,⁴² and their genetic signatures are very similar to that of Persians, nearly obscuring their original population foundations of U.S. and U.K. cats.

Many cat breeds originated from single gene traits found in western European random-bred, feral cat populations, such as the folded ears of the Scottish Fold²⁸ and the dorsally curled ears of the American Curl.⁵⁸ Controlled breeding and selection of these cats slowly developed the populations into a unique breed, based on conformation as well as the original unique trait. Many newly identified spontaneous mutations that produce unusual traits, such as ear folding or curly fur, are generally recognized in random-bred, feral cat populations, followed by morphologic molding using various desired combinations found in other breeds. Thus many new and some established breeds have allowable outcrosses to influence their “type” and to support genetic diversity in the breed foundation. For example, genetic differentiation of the Scottish Fold and the British Shorthair is difficult because the two are allowed to interbreed to maintain diversity and to modify type. Because Persians have a highly desired brachycephalic head type, this breed tends to influence many other newer breeds. Breeds in which the dolichocephalic type is desired are often outcrossed with the Siamese family of cats. Hence the newly developing breeds can inherit health problems from the foundation breeds. For example, newer breeds such as Burmilla and Asian will likely have the same concerns for polycystic kidney disease as the Selkirk Rex and British Shorthair because of outcrossing with the Persian, which is desired for the production of the brachycephalic head type.

The outcrosses that are valid for any breed can vary among cat registries, and the same breed may even have a different name depending on the country or registry. For example, the Burmese registered by the GCCF² in the United Kingdom and FIFe²² in Europe is known as the Foreign Burmese breed in the United States, and these cat “breeds” have significantly different craniofacial type among the countries. The Havana Brown has developed into a distinctive breed in the United States, also with a significantly different craniofacial structure than its foundation breeds, the Siamese and Oriental Shorthairs. However, in Europe the chestnut color variety of the Oriental Shorthair is similar to (basically identical to, in fact) the Havana Brown. Some breeds, such as Korats and Turkish Vans, have very similar standards across almost all countries and registries. However, breeds with similar standards may be different in different countries because their breeding histories are different, even though similar-looking cats have resulted from the selection process.

During the world wars cat breeding was not a priority, and many breeds became nearly nonexistent in Europe. To reconstitute the breeds in the early 1950s,

many European breeds have been re-established with substantial crossbreeding and outcrossing using a concoction of breeds and feral populations as stock. Thus the genetics of breeds in the United States, which did not suffer such an extreme population crash, may be quite different from that of the same breeds in other parts of the world. For example, Burmese in the United Kingdom and Australia suffer from a heritable hypokalemia, whereas American Burmese do not^{32,35} but instead have a recessive craniofacial defect in some prominent lines.⁴⁹ The worldwide regional differences of the cat breed histories should be considered with their health care management.

ORIGINS AND BREED HEALTH

Overall, from a phylogenetic point of view, cat breeders are “splitters” instead of “lumpers,” and a few foundation breeds encompass most variation of cat breeds. More cat breeds are documented than can be genetically defined. In addition, the world’s cat populations can be defined as only approximately eight populations (Figure 42-2). These world cat populations still mimic human migrations, some populations being distinct in areas of the world that have less European and Asian migration, such as Iran. The early descriptions of some cat breeds are genetically supported even today. Cats from Siam and Burma are represented by breeds such as the Korat, Siamese, Burmese, and Birman. Individuals from these breeds show strong genetic relationships with feral cats from Southeast Asian but not Western Europe, which strongly suggests that these breeds did originate in the Far East. For some breeds, such as the Japanese Bobtail, the origin of the tail trait does seem to be in Japan, although genetic influences from western cats have obscured its true origins. Like breeds within a breed family, genetically influenced health concerns could originate and be prevalent in the feral cat populations that are the origins of some modern breeds.

Some cat breeds are going “back to their roots”; the breeders have become concerned with genetic health and are proactively improving the size of their gene pools. Because genetic testing now allows the identification of cats that carry undesired aesthetic traits, such as certain coat colors and fur lengths, cat breeders are more open to outcrossing cats and then using genetic tests to prevent the undesired qualities. Breeders are now more willing to import cats from the countries of origin to add needed genetic diversity for health and also to help the selection process of type, behavior, and other important qualities of a cat breed. Two studies have presented the genetic diversity and inbreeding levels in domestic cats,^{39,45} and both suggest that some breeds have more diversity than others and some breed management from the genetic point of view may be necessary (Figure 42-3).

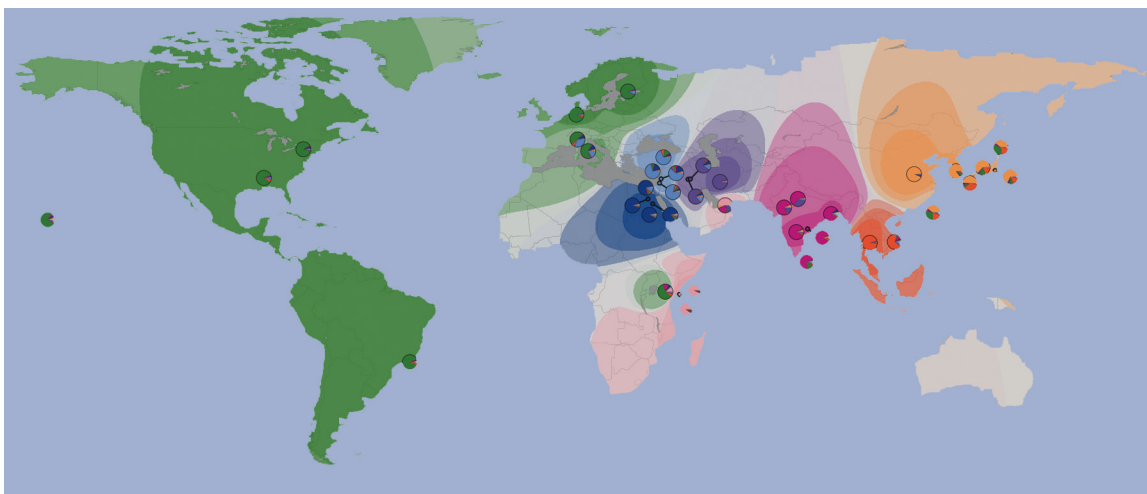


FIGURE 42-2 Population structuring of the world's random-bred cats. Bayesian clustering was used to define the world's cat populations. By using both single nucleotide polymorphisms and short tandem repeat markers (STRs; microsatellites), eight modern random-bred lineages can be defined from the world's random-bred cat populations. The pie charts represent the percentage of the eight worldwide lineages found at each location. The shading indicates the strength of the predominating lineage for each region of the world. The world's cat populations are parsed into the following categories: European/Americas (*green*), Eastern Mediterranean (*light blue*), Egypt (*blue*), Iraq/Iran (*purple*), West Indian Ocean (*pink*), India (*red*), Southeast Asian (*orange*), and East Asian (*light orange*) cats.

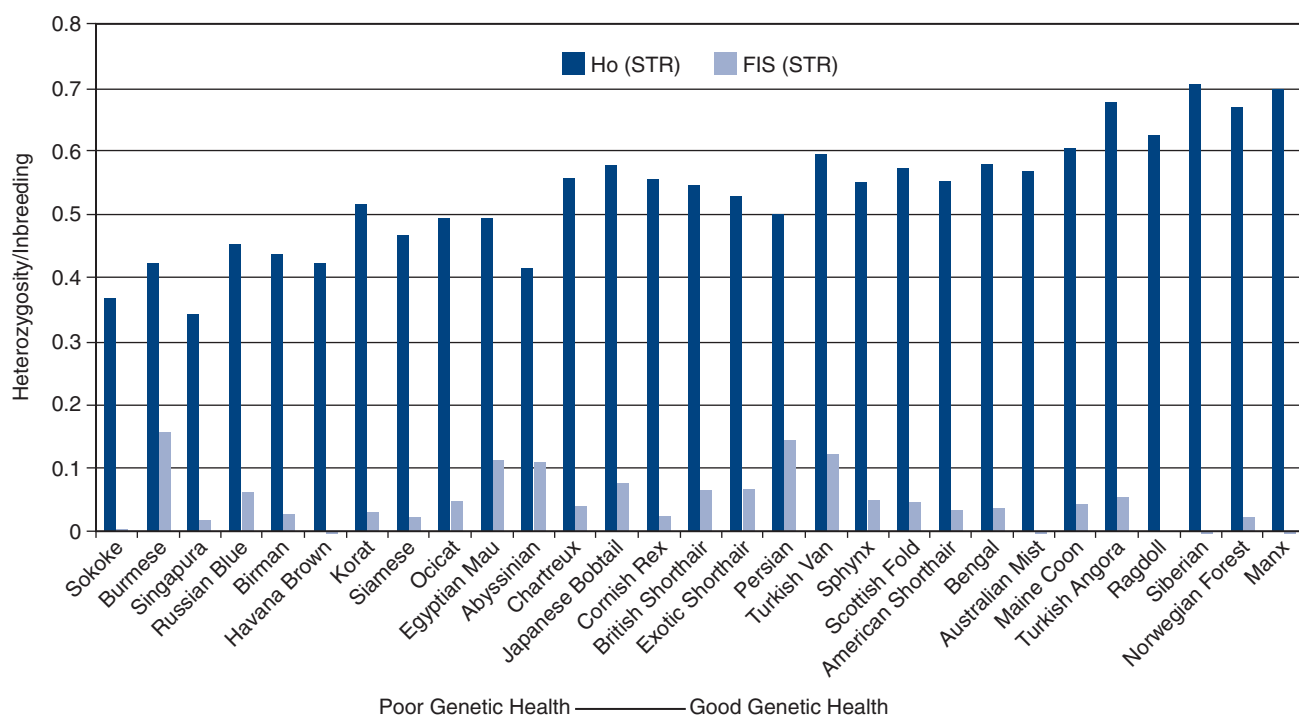


FIGURE 42-3 Relative genetic health of domestic cat breeds. A variety of genetic markers and population statistics are used to measure a population's genetic diversity. Short tandem repeat markers (STRs; microsatellites) and single nucleotide polymorphisms (SNPs) were used to calculate the genetic variation of cat breeds, measured as heterozygosity and inbreeding Wright's coefficients (F_{IS}). Presented are the heterozygosity values and inbreeding coefficients based on STRs for the breeds. Additional statistics were also calculated, including the SNP-based heterozygosity and inbreeding coefficients and the effective number of alleles for each type of genetic marker. The relative rank for each measure was determined for each breed and then averaged to determine "overall genetic health." The overall genetic health is represented from poor health on the *left* to good health on the *right*.

The availability of genetic tests and standardized markers for parentage testing³⁸ supports outcrossing and cat breed management. These same tools can be assets to veterinarians as they assist clients with the health management of their cats.

In conclusion, veterinarians should be knowledgeable about the relationship of cat breeds in their country and also be aware of regional differences in breeding practices. Many cat breeds are genetically distinct and genetically diverse, leading to fewer health problems. However, other breeds do harbor low genetic variation, which may be detrimental if the population is susceptible to a new viral or bacterial strain. Inbreeding depression can lead to a distinct health concern or just the overall poor health of the population. Knowledge of breed relationships and cross-breeding programs can help predict the potential spread of breed-related or breed-specific diseases across the cat fancy.

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