CHAPTER 3

CATS

I HAVE ROUGHLY EQUAL AFFECTION FOR CATS AND DOGS, which puts me in a distinct minority among people of my acquaintance; most are quite partisan in their allegiances. But I am currently living with a cat person, so I have a cat sitting on my lap as I write this. His name is Sylvester because he looks so much like the hapless *Looney Tunes* character with the black tuxedo coat, perpetually tormented by an extremely neotenic bird named Tweetie. Sylvester also shares some of the cartoon character's haplessness: he is ungraceful, if not downright clumsy; once, while soundly sleeping, he actually fell off the top of the couch onto my prone chest, then, in terror, leaped over to an adjacent couch but misjudged and crashed ignominiously on the hardwood floor, from which he strenuously but unsuccessfully sought to gain traction for rapid egress, as if it were an ice surface, and then, upon finally getting his legs, bumped into a cedar chest. (He left me, as a memento, two sets of superficial gouges on my chest and an adrenaline boost.) Sylvester has other problems as well, including a morbid fear of doorbells and the people who subsequently appear. When the doorbell rings, he makes a dash for the closet or the underside of the bed.

Sylvester's sister, Smoke—a gray tuxedo—in stark contrast, is as graceful and athletic a creature as I have ever known. She could do a complete somersault when she was six months old, and she can rest on her hind

legs like a meerkat. She is a gray blur when chasing a laser pointer up and down stairs. Sylvester can only watch until she tires. Smoke is also much more "well adjusted." She loves strangers, sidles up, tail high and shivering seductively or plopping on her back for a belly rub.

When we first brought them home as kittens, Smoke exited the carrier immediately and started exploring; Sylvester wouldn't budge. I finally had to dump him out after an hour. When we moved from one part of Brooklyn to another, Smoke mostly took it in stride; Sylvester was a wreck for weeks. If it weren't for Smoke's calming influence, it would have been much longer. For Sylvester is exceedingly fond of his sister and, for the most part, vice versa. When they were respectively spayed and neutered, Smoke and Sylvester were placed in the same recovery cage, primarily for Sylvester's sake. When Smoke had an emergency medical procedure to extract yarn from her intestine, Sylvester was in distress during her absence, incessantly calling for her. They often sleep in a ball so tightly bound that it is difficult to discern their outlines. Their relationship has greatly altered my prior notions of cat sociality. The solitariness of cats is greatly exaggerated.

Sylvester and Smoke were also instructive with respect to a behavioral syndrome that plays an important role in the domestication process—a personality dimension in cats, humans, and many other vertebrates, from goldfish to pigs, called the shyness–boldness continuum. Sylvester is on the shy end, Smoke on the bold end. Since they shared a womb and have spent all but one day of their life together indoors, it is tempting to attribute all of their personality differences to their genes. But Smoke and Sylvester had a rich and formative, albeit brief, existence before we adopted them at 10 weeks of age, which undoubtedly influenced their personalities.[1]

The shared experiences of Smoke and Sylvester—first as kittens handled a lot by humans, and then as coddled indoor cats—also no doubt contributed greatly to their temperament, and particularly their reaction to humans. If Smoke had been born feral, she would not be as human friendly as she is today. And that is true of Sylvester as well; in the big scheme, he is not that shy.

Figure 3.1 Meet Sylvester. (Photo by author.)

Our neighbor is part of an innovative program—called trap-neuter-release—to deal with feral and semiferal cats, which abound in this city and elsewhere around the globe. These cats are provisioned and then captured, spayed or neutered, and returned to the empty lots or abandoned buildings from which they came. This method is actually better—and more humane—for controlling the feral cat population than is simple removal.

Prior to her move to New York City, our neighbor worked with feral cats in the Virgin Islands. She adopted three of them. Though they, too, vary in their shyness, compared to these three formerly feral cats Sylvester is quite bold. One of them, also a black tuxedo, called Baby, I have glimpsed only briefly. The difference between Sylvester and Baby is largely due to the different environments in which they grew up. Around humans, the boldest feral cat is shyer than the shyest home-reared one, even if the feral cats are adopted soon after weaning. As with canines, there is a window of socialization, and in cats it seems to close earlier and more firmly than in dogs.

There is an interesting trend among the three feral cats related to the age at which they were adopted. One of them, Pablo, was aban-

doned between 4 and 6 weeks of age, which is prior to normal weaning. Though still shyer than Sylvester, he is by far the boldest of the three feral adoptees. Lucy, who was adopted at about 12 weeks of age (two to four weeks after cats are usually weaned) is much shyer; and Baby, adopted at a slightly older age, is shyer still. Early human handling, especially during the preweaning period, is crucial to a cat's later reaction to humans.

I use the term "feral" loosely here, for the "alley" cats in both the Virgin Islands and New York City are probably relatively recent arrivals to the street; many are second- or third-generation descendants of abandoned cats and were provisioned to varying degrees. Truly feral cats must secure all of their calories unaided (consciously) by benevolent humans and have bred for many generations under these conditions. It is difficult to determine how many truly feral cats exist in New York City—perhaps a relative few. You are more likely to find them in more rural settings. We would expect a truly feral cat adopted at the same age as Baby to be even less given to human interaction. But even these truly feral cats would seem "friendly" compared to the wild ancestors of all truly feral cats, semiferal cats like Baby, and pampered house cats like Smoke and Sylvester. Because of genetic psychological alterations wrought by the domestication process, even the most feral cats are more human friendly than true wildcats raised under the same conditions.

The domestication of cats, though, has been much less pronounced than that of dogs. Even Sylvester more closely resembles his wild ancestors, both physically and psychologically, than do the most wolflike dog breeds. Generally, there is more wildcat in domestic cats than there is wolf in dogs, because cats took a somewhat different route to domestication than dogs. Yet there are important features common to both. The differences and similarities in the domestication of dogs and cats have a lot to do with the prior evolutionary history of wolves and wildcats, respectively. We explored the evolutionary history (genealogy) of wolves in Chapter 1; let's now consider the evolutionary history of wildcats.

THE CAT FAMILY

Though cats and dogs belong to the same mammalian order, Carnivora, they come from two quite distinct branches (Figure 3.2). The dog branch includes—in addition to other canids—bears, raccoons, otters, skunks, seals, and sea lions. The cat branch includes—in addition to other felids—hyenas, mongooses, and civets. Perhaps what most distinguishes the cat branch from the dog branch is that the members of the cat branch are more exclusively carnivorous; their diet includes very little plant material. The relative specialization of the cat branch is most pronounced in the cat family, Felidae. Felids are considered obligate carnivores, in that they can metabolize only animal protein.

Several distinctive features of felids reflect their meat dependency—most obviously, their teeth. All carnivores have modified premolars and first molars specialized for scissor-like shearing, called carnassials. The size of the carnassials relative to molars provides a good indication as to how much of a carnivore's diet is meat-derived protein. In bears (family Ursidae), the carnassials are small and the molars large, in accordance with their largely vegetarian diet. The size of the molars reaches its extreme in giant pandas, which rely exclusively on bamboo. In dogs

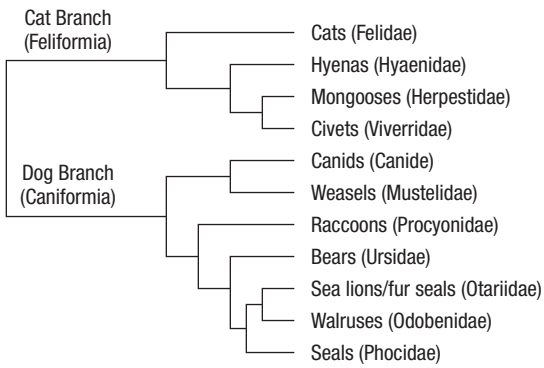

FIGURE 3.2 Carnivore phylogeny with family relationships. (Redrawn from information by Dr. David L. Atkins and by Arnason et al. 2001.)

(family Canidae), both the carnassials and the molars are large, reflecting a diet relatively balanced between meat-based proteins and plant-based carbohydrates. In felids, the carnassials are even larger than those of dogs, and the molars are vestigial. Felid canine teeth are also larger than those of canids, and their incisors sharper. Their dentition is so specialized for cutting that felids, including domestic cats, can't chew.[2]

Perhaps the greatest evolutionary innovation of the felids is in their claws. Whereas dogs and bears walk on the soles of their feet, cats actually walk on their toes, which provides a mechanical advantage in walking and running, through greater stride length. This mechanical advantage in felids is one reason the fastest saluki or greyhound could never beat a cheetah in a 100-meter dash. But toe walking potentially poses a problem in abrading and hence dulling the claws. That problem was alleviated through the evolution of retractable claws. Each claw is controlled by one muscle above that, when contracted, retracts the claw, and one muscle below that, when contracted, releases the claw. When a cat walks, the claws are retracted, which keeps them sharp for the occasions when they need to be deployed.

In contrast to canids, felids are largely ambush predators and kill with a single bite to the skull, jugular, or spine, depending on the size of the prey. The jaw muscles of felids are proportionally larger than those of canids; hence they can generate greater bite force, which also makes them more efficient killers.[3] If you were a wildebeest, you would much rather be killed by lions than by African wild dogs, because death by lion is faster and less painful. Wild dogs seem to take forever to kill large prey—death by a thousand small bites; they often start consuming their beleaguered prey long before it finally dies. Even the most unpracticed lions get the job done much more "humanely."

There is only one feline, the lion (*Panthera leo*), that is a truly social and a cooperative hunter, though cheetahs (*Acinonyx jubatus*) hunt together on occasion.[4] All other 35 felid species, including the ancestors of the domestic cats, are solitary hunters and live a largely solitary existence.

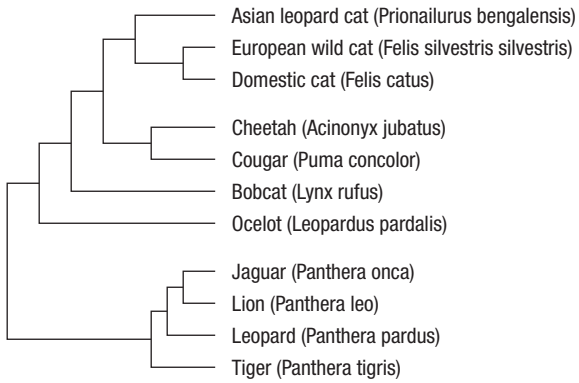

FIGURE 3.3 Felid phylogeny. (Adapted from Johnson et al. 2006.)

The family Felidae first entered the evolutionary stage about 35 million years ago (henceforth abbreviated "mya"), at the very end of the Eocene epoch (of the Cenozoic era). The last common ancestor of all modern felids lived in Eurasia about 11 mya (Miocene epoch), from which eight distinct lineages evolved (Figure 3.3).[5] The first lineage to split off (about 10.8 mya) included the great roaring cats of the genus *Panthera* (tiger, lion, leopard, snow leopard, and jaguar) plus two species of clouded leopards (*Neofelis*). The lineage that includes the domestic cat (genus *Felis*) originated about 6.2 mya (in the late Miocene).

About 2 mya the wildcat, *Felis silvestris*, split from other members of the genus *Felis*. This is the wild ancestor of the domestic cat. Like the wolf, the wildcat has a wide distribution, which includes much of Eurasia and Africa; north to south it extends from Scotland to the Cape region of South Africa; west to east it extends from Iberia to Mongolia. Over this wide range, five distinct subspecies evolved: the European wildcat, *Felis silvestris silvestris*; the central Asian wildcat, *Felis silvestris ornata*; the Near Eastern wildcat, *Felis silvestris lybica*; the Chinese mountain cat, *Felis silvestris bieti*, and the African wildcat, *Felis silvestris cafra*[6] (Figure 3.4). There had long been debate as to which of these subspecies was the ancestor of the domestic cat, which was recently decided in favor of the Near Eastern wildcat (*F. silvestris lybica*).[7]

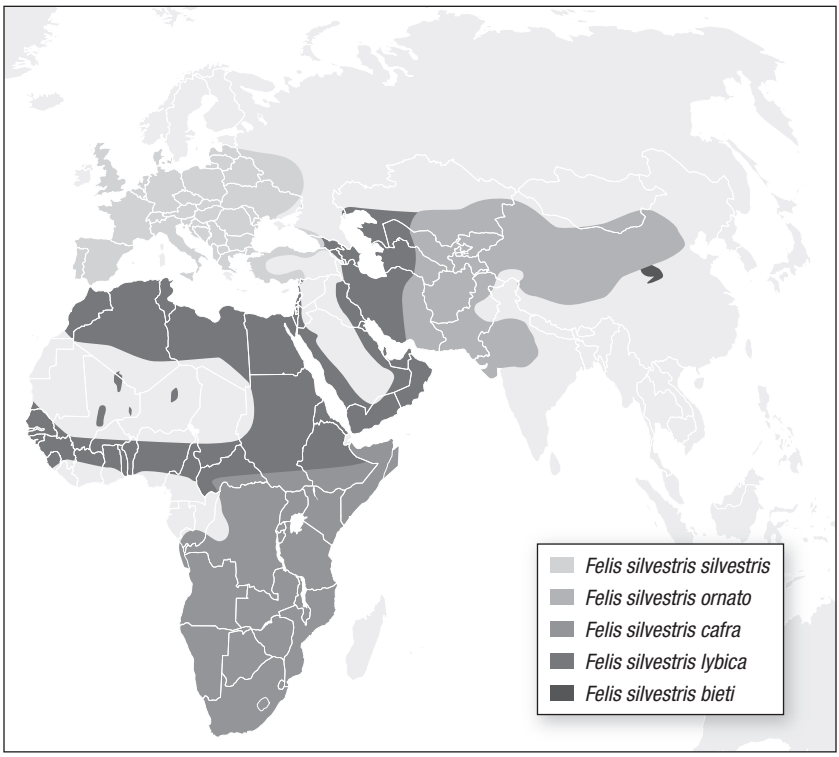

FIGURE 3.4 Geographic ranges of wildcat subspecies.

The Near Eastern wildcat is a typical felid in its basic body plan, specialized meat diet, solitary existence, and defense of exclusive territories, in all of which respects it differs from the wolf. These traits also make cats unlikely candidates for domestication and explain in large part the divergent route this process took. For cats are almost entirely self-domesticated through the process of natural selection. Only very recently have a small fraction of the 600 million cats in the world today been subjected to artificial selection for human ends.

Of the five wildcat subspecies, the Near Eastern wildcat is among the more tolerant of people, but that probably wasn't a huge factor in determining why this subspecies alone was domesticated. Contingent historical factors in its interactions with humans figure much more importantly in the domestication of this subspecies.[8]

THE MOUSE CONNECTION

It was long thought that the Near Eastern wildcat was first domesticated in Egypt.[9] But recent archaeological and genetic evidence points elsewhere. The genetic evidence, which is based on mitochondrial DNA collected from individuals throughout the range of this subspecies, indicates that Near Eastern wildcats were first domesticated in the cradle of agriculture, called the Fertile Crescent, about 10,000 BP.[10] It was here that humans first began to store grains. These stored grains proved vulnerable to a recent invader from northern India, called the house mouse (*Mus musculus*). For the wildcats in the area, these house mice were a new reliable food source, so some wildcats began hanging around human settlements. These pioneers in the domestication process did not require human encouragement, but they had to surmount a significant psychological barrier. The barrier was an evolved fear of humans and other large predators, including the village dogs. Only those wildcats that could surmount this fear could effectively exploit this new resource.

In essence, human agrarian settlements provided the wildcats in the area a new niche, which required different behavioral dispositions than the old relatively human-free niche had required. Through natural selection for tameness, a subset of the wildcats was able to increasingly thrive in this new niche. But in contrast to dogs, which also exploited this niche, even the more tame wildcats retained their previously evolved hunting skills and equipment. For example, their canine teeth did not diminish in size as they did in village dogs.[11] These relatively tame cats could also still hold their own against the untame wildcats in the area in any dispute. And this was probably true long after the domestication process commenced.

The first evidence that the cat-human relationship had progressed beyond one of mutual convenience is a cat burial in Cyprus 9500 BP.[12] This cat was buried right next to the grave of a human and oriented in

the same direction. Cats are not native to Cyprus, so they must have been transported there by humans. And since cats are not effective stowaways, like mice or rats, they must have been transported deliberately. Moreover, the cat burial suggests that they were no longer confined to granaries, but were more intimately associated with households. Household cats require both a greater degree of tameness and more active human encouragement.

There is a large gap in the archaeological record after the Cyprus burial, aside from a couple of teeth from Israeli archaeological sites. A small ivory statue from Israel, dated 3700 BP, indicates that the cat-human relationship had become increasingly intimate during the intervening years. It is only after 3600 BP, at the beginning of the New Kingdom period, that cats appear in Egypt.[13] But though domestic cats didn't originate in Egypt, it was there that domestication was taken to the next level.[14]

During this Egyptian "Golden Age," paintings of cats become increasingly common. In some, cats are depicted with collars, sometimes eating out of bowls; so some Egyptian cats, no doubt mostly those of royalty, were spending lots of time indoors.[15] This royal connection led eventually to cat veneration by 2900 BP, and then to deification in the form of the goddess Bastet.[16] When Herodotus visited Bastet's sacred city, Bubastis (2525 BP), the temples to Bastet there were crawling with pampered cats.[17]

Though deification has its perks, there was also a price to be paid. Sacred cats were sacrificed in great numbers for ritual purposes, mummified in the Egyptian fashion, and buried in huge cat cemeteries, which came to contain tons of cat remains.[18] Because of the huge scale of cat burials, it is surmised that the Egyptians must have been actively breeding domestic cats at this time. Whether this breeding was selective—that is, true artificial selection—is not clear, though Patrick Bateson and Dennis Turner hypothesize that the large population of cats in northern Egypt could well have been selected for increased sociability.[19]

Though Egypt had outlawed their export, domestic cats could be found in ancient Greece by 2500 BP.[20] The Romans took control of the Nile Delta and the rest of northern Egypt in 2030 BP, and from their port city of Alexandria domestic cats were transported throughout the empire on grain ships. To protect the grains shipped out of Alexandria from mice, ships were inoculated with domestic cats, some of which probably abandoned ship—in keeping with their independent dispositions—in far-flung ports.[21]

In any case, cat colonies were soon established in many port cities, from which cats worked their way inland. This inland movement was probably also human aided, as, left to their own devices, cats are not prone to move far from where they were born. By 1000 BP, domestic cats were common in Europe.[22] Domestic cats didn't reach the Americas until much later—perhaps as early as the voyages of Christopher Columbus (1492–96), perhaps not until the voyage of the Mayflower (1620); they are thought to have reached Australia by way of European explorers in the seventeenth century.[23]

The eastward movement of domestic cats also commenced during the Roman Empire, along trade routes between Rome and China. By 2000 BP, domestic cats could be found in China and India.[24] From China the domestic cat worked its way through continental Southeast Asia, then much of island Southeast Asia. While the westward movement of domestic cats, through the Mediterranean region to northern Europe, traversed areas with indigenous wildcat populations, there were no such wildcats along much of the eastern route, including most of India, China, and all of Southeast Asia. So, while western domestic cats continued to interbreed to varying degrees with indigenous wildcats, the domestic cats of the Far East evolved in isolation. The result was several distinct landraces, largely distinguishable by distinctive coat color patterns, such as the Siamese, Korat, and Birman.

GENETIC DRIFT AND NATURAL SELECTION

Just as domestic dogs became differentiated into distinct landraces, so, too, did domestic cats, albeit to a much lesser degree. In the differentiation of these Southeast Asian landraces, the other major evolutionary process, genetic drift, figured more prominently than natural selection.

In genetic drift, populations diverge by means of random genetic alterations that are selectively neutral, meaning that they don't affect fitness. Such is the case, for example, with the genes that underlay color variations of Siamese, Korat, and Birman landraces. Genetic drift is ubiquitous but varies with population size. The smaller the population, the more genetic drift, simply because random influences of any kind are more pronounced in small populations; this is what statisticians call "sampling error."

Evolutionary biologists refer to "effective population size," which is roughly the number of potentially interbreeding individuals. Genetic communication from one population to another, called "gene flow," increases the effective population size, up to that of the combined populations. So, genetically isolated populations, in which there is no such gene flow, are more prone to genetic drift. For domestic landraces it is important to consider not only gene flow between landraces but also gene flow between wild populations and landraces. As long as there is any gene flow between wild populations and domestic landraces, genetic drift is restricted. But when wild populations are absent, as for cats in Southeast Asia, conditions are ideal for genetic drift. The color variations among the Siamese, Korat, and Birman landraces are most likely the result of genetic drift that was later reinforced by artificial selection.

Natural selection, though, was also operating on the Southeast Asian landraces as elsewhere. For example, the short hair common to the Southeast Asian breeds and others, such as the Abyssinian, is likely the result of natural selection for reduced heat retention in a warm climate.

So, too, perhaps, were their characteristically long, slender bodies, which lose heat more rapidly than the stocky body type called "cobb." And the long hair and cobb body type that are characteristic of northern landraces, such as those ancestral to the Maine coon, Norwegian forest cat, and Siberian, are at least partly adaptations to colder climes.

All of the landrace-derived breeds mentioned in the preceding paragraphs are categorized as "natural," in that they were developed with minimal human aid by way of artificial selection and hybridization.[25] As was true of "ancient breeds" in dogs, the term "natural breeds" is problematic. The Abyssinian, Egyptian Mau, and Chartreux, for example, are considered natural breeds but are in fact recent (phenotypic) reconstructions of indigenous landraces.[26] The Japanese Bobtail and American shorthair are, on the other hand, better candidates for the "natural breed" appellation.

Some of the natural breeds are hundreds of years old, but most domestic cat breeds are of a much more recent vintage—the last half of the twentieth century. It was only then that cat fanciers really got to work and cat shows—modeled after dog shows—escaped the limited orbit of aristocrats.[27] A number of "fancy" breeds were created in the 1960s, including the Scottish Fold, the Sphinx, and the Ocicat.[28] In the 1970s came the Singapura and the Australian Mist; the 1980s brought us the York Chocolate, the California Spangled, the Burmilla, the Nebelung, and the Donskoy, among other new creations. The Ragamuffin was created in the 1990s, while the Levkoy, which is shudder-inducingly ugly, is a twenty-first-century creation.[29] By the middle of this century, the number of existing cat breeds—currently more than 60—may well double.

HOW FANCY CATS WERE CREATED

A number of fancy cat breeds began with a mutation—often confined to one individual in a litter—that had an obvious effect on the phenotype. The Scottish Fold, for example, was founded by a barn cat from

Perthshire, Scotland, with peculiarly forward-bending ears.[30] Someone decided it would be a good thing to perpetuate this mutation. The Manx, from the Isle of Man, has a skeletal mutation that causes the tailless condition, among its other effects. In this it somewhat resembles the Japanese Bobtail, a natural breed with a quite different mutation.[31] Munchkin cats have a mutation that causes limb shortening analogous to that of the dachshund.[32]

Polydactyl cats have extra toes and constitute a recognized breed in the United States, called the American Polydactyl.[33] They seem to have originated in southwest England, from where they made the Atlantic crossing by ship to New England, where they are especially abundant. One important reason for their early success was the widespread belief among sailors that they brought good luck—another example of the role of human caprice in the domestication process. The record for polydactyly is 27 toes, set by a Canadian cat.[34] Here's hoping that the record isn't broken.

There is another mutation, called radial hypoplasia (RH), or "hamburger feet," which results in a different form of polydactyly, of a spiraling nature.[35] A creative breeder in Texas sought to build on this deformity in constructing a "Twisty cat" breed, in which the spiraling extends to the bones of the forelimb. Twisty cats also have extremely short forelimbs and relatively long hind limbs, which cause them to sit like a squirrel—hence an alternative name, "squitten." Twisty cats are banned in Europe on humanitarian grounds, but not in the United States; the same is true of the Munchkin. It is time that the United States caught up with the United Kingdom in this regard. The deliberate breeding of skeletally deformed breeds is unconscionable.

Some of the oddest-looking breeds result from a mutation that causes hairlessness. Actually, these cats aren't completely hairless; they just look that way. The first such breed originated in 1966 from a single naked kitten, appropriately named Prune.[36] It is a mystery to me why anyone would want to perpetuate this condition; I suspect it is simple neophilia.

Given the climate there, it is particularly perverse that the Sphinx is a Canadian breed. But then, two other notable hairless breeds, the Donskoy and Levkoy, were created in Russia and Ukraine, respectively. One hopes they are indoor cats. Other cat breeds were founded by less drastic mutations of the coat, including the Cornish Rex (downy hair), Devon Rex (short guard hair), Iowa Rex (dreadlocks), and American wirehair (dense wiry coat).[37]

The other method for generating new cat breeds is hybridization with existing breeds. The Siamese is most commonly used as one part of the cross. For example, the Havana Brown was the result of a cross between Siamese and American shorthair, and the Himalayan represents a cross of Siamese and Persian. Second-, third-, and fourth-order hybridizations begun with Siamese hybrids and other breeds include the Ragamuffin, Ocicat, and California Spangled. Some notable hybrids that lack a Siamese component include the Australian Mist (part Abyssinian), the Nebelung (part Russian Blue), and the Burmilla (part Burmese). The Levkoy is noteworthy not only for its uncomeliness but for the fact that it was created from a cross of two mutant breeds (the ear-challenged Scottish Fold and the hair-challenged Donskoy). The mutant ante can be ever upped.

Some truly creative breeders decided to go outside of the domestic cat box in finding partners for hybridization. The Chausie is a cross between an Abyssinian and a jungle cat (*Felis chaus*). Since the jungle cat is in the same genus (*Felis*) as the wildcat and the domestic cat, it is not surprising that this match worked. But other crosses outside of the genus *Felis* are more ambitious. The Bengal is a cross between a domestic cat and a leopard cat (*Prionailurus bengalensis*). At least the leopard cat is about the same size as a domestic cat; not so two other out-of-genus crosses: the Caracat is a cross between an Abyssinian and a caracal (*Caracal caracal*); and the Savannah is a cross between a domestic cat and a serval (*Caracal serval*).[38] Both caracals and servals are considerably larger than wildcats.

INBREEDING AGAIN

When you start a breed with a single mutant, you have a founder population of two: the mutant and the individual with which it mates. To maintain the mutation at high levels, you must mate close relatives—say, siblings, or mothers and fathers with sons or daughters. Either way, the result is intense inbreeding and the accumulation of deleterious recessive mutations—a phenomenon known as "inbreeding depression." Indeed, inbreeding in some cat breeds begun in this way is as severe as in dog breeds, as reflected in breed-characteristic pathologies.

The opposite occurs when breeds from different species are crossed, as in the Savannah and Caracat. Here the problem is a lack of harmony of various sorts among the genomes—a condition known as "outbreeding depression."[39] Servals and domestic cats, for example, don't have the same number of chromosomes, which creates fundamental problems in partitioning them during the creation of sperm and eggs. More subtly, certain suites of genes that work particularly well with each other are normally inherited more or less as a unit. These "coadapted gene complexes" are broken up with excessive outbreeding.

The optimal condition lies somewhere between these poles, when the porridge is neither too cold nor too hot. The "just right" porridge is called hybrid vigor. This is what you get in mongrel dogs and barn cats. (Sylvester and Smoke are American shorthairs whose mother was the latter.) You would also expect to get hybrid vigor from crossing two distinct cat breeds, such as were used to create the Himalayan (Siamese × Persian). And initially, you do. The problem is that only a relative few offspring of these crosses, which have the desirable characteristics, are used as breeders for the next generation. The intense artificial selection for these characteristics soon results in inbreeding depression again.

The so-called natural breeds were in the "just right" hybrid vigor mode until cat fanciers began to control their breeding in the twentieth

century. The effects of these efforts are especially evident in the Siamese, long the most popular of the natural breeds. The Siamese in Europe and North America today are strikingly different from those found in Thailand, as I can attest from personal experience.[40] The Thai Siamese is a larger animal and longer of leg. Though the Thai Siamese has the typical "oriental" lithe body, it is more muscular, and not nearly as thin as that of the western Siamese. In addition, its skull is larger and notably more rounded in shape. These differences reflect the effects of artificial selection in the West.

The first Siamese to arrive in the West—appropriately named Siam—was an 1878 gift to President Rutherford B. Hayes.[41] Six years later the first breeding pair was imported to Britain, followed by several more imports of a small number of these cats. Most Siamese in Britain today may be the descendants of only 11 imported Siamese. This small founder population, with its inherent sampling error relative to the genes of the Thai Siamese, was then prone, by virtue of its small size and isolation, to further random divergence through genetic drift.

The novel Siamese were an immediate hit at cat shows, so they were newly subjected to artificial selection, by means of which they further diverged from the original type. This divergent evolution accelerated in the last half of the twentieth century because judges came to prefer longer, thinner cats with proportionally small heads of a triangular shape, topped by large ears, set wide to emphasize this triangularity—to which end the snout was also thinned and the eyes became more almond shaped. Within a few decades, traditional Siamese had disappeared from cat shows (see Figure 3.5). Some breeders organized to preserve the "traditional" style of Siamese, which is now recognized by TICA (The International Cat Association) as a new breed, called Thai. Such are the inversions of the topsy-turvy world of cat breeders.

The effects of inbreeding have been dire. Siamese have cancer rates rivaling those of Bernese mountain dogs and other cancer-prone dog breeds. They are especially prone to breast cancer. Accordingly, the life span of the Siamese is considerably shorter—with a median length of

FIGURE 3.5 Thai Siamese (left) and European Siamese (right). Note the differences in the skull and face. (Thai Siamese [left]: © iStock.com/Lena Kozlova. European Siamese [right]: © iStock.com/IvonneW.)

10–12 years in one study—than that of the average house cat (15–20 years). Other "natural breeds," such as the Abyssinian, also have shortened life expectancies as a result of inbreeding. Those that live longest are prone to blindness by means of progressive retinal atrophy and other defects of premature aging.

Aside from the Siamese, the Persian and the Himalayan have been the breeds most modified by sustained artificial selection. In addition to their gorgeous long hair, these two breeds are notable for their brachycephalic (squashed) faces, first developed in the Persian and inherited in the Himalayan when it was created through Siamese × Persian crosses. Since creation of the Himalayan, the brachycephaly has been further exaggerated in both breeds, with predictable results. Though neither breed rises to the level of bulldog grotesquerie and its concomitant ailments, they do suffer from breathing problems, chronic sinus infections, and, more generally, abbreviated lives.

In stark contrast, the American shorthair, of which Smoke and

Sylvester are exemplars (OK, just Smoke), is a natural breed that has remained a natural breed. Which means that American shorthairs have long bred with whomever they deemed desirable—and the females often find it desirable to mate with more than one male. They evolved, from a large founding population, by means of natural selection into the perfect domestic cat—robust, athletic, and low maintenance. If properly socialized, they make ideal house cats. As an added bonus, American shorthairs are among the best mousers, right up there with the legendary Egyptian Mau.

There is an attempt under way to create an even better mouser, which would be the first cat breed created for function rather than appearance. The breed is called American Keuda, which is an acronym for "Kitten Evaluation Under Direct Assessment."[42] The breed is being created from American shorthair barn cats. The only criterion for the breeding program is exceptional mousing ability. Inbreeding, which inevitably reduces this ability, is therefore kept to a minimum, as evidenced by the huge variability in coat colors. Interestingly, some Keudas have come to look very much like the Egyptian Mau, a cat breed that perhaps most resembles the ancestral *Felis silvestris lybica*, from which all domestic cats are descended.

CAT GENOMICS

Cat genomics is not nearly as far advanced as dog genomics; it is still in the kitten stage. The first complete cat genome sequence came from an Abyssinian named Cinnamon.[43] Subsequently, 10 other breeds have been partially sequenced. There are clear geographic factors in the genetic similarities of cat breeds. The Southeast Asian breeds, for example, form a distinct cluster; the European and North American breeds form a less distinct cluster; and the Central Asian, West Asian, and North African breeds tend to clump as well. Exceptions, such as the Ragdoll, American Curl, Ocicat, Sphinx, Devon Rex, Cornish

Rex, and Bengal, are generally Western breeds recently created through hybridization or major mutations.

Many of the major mutations affecting body type and coat coloration of domestic cats were identified in the pregenomic age by conventional linkage analysis.[44] Here I will consider a few interesting recent discoveries concerning coat characteristics.

Recall that a mutation (in a gene called *Fgf5*) was responsible for long hair length in many dog breeds. A mutation in the same gene also appears to cause long hair in cats.[45] Actually, four separate mutations in this gene can cause long hair in cats, each different from the mutation that causes long hair in dogs. This phenomenon—same gene, different mutation, similar phenotype—is actually quite common. It occurs when different mutations, causing different amino acid substitutions in the coded protein, disrupt biological activity in similar ways. Since each variant of a gene is called an allele, we can more concisely say that, in this case, different alleles result in the same phenotype.

But it is more often the case that different mutations in the same gene have different developmental effects; that is, different alleles result in different phenotypes. Consider the tyrosine gene (*TYR*), which plays an important role in coat pigmentation. One mutation in this gene is largely responsible for the distinctive coloration of the Siamese: dark extremities, light body.[46] This color pattern is due to the fact that the mutant allele is temperature-sensitive. During development, the extremities are cooler than the rest of the cat and the *TYR* gene is more active; in the more central areas, where the body is warmer, the *TYR* gene is less active, given this mutation. A different mutation in this gene results in an allele that is less temperature-sensitive.[47] The result is the Burmese color pattern, in which the nonextremities are more pigmented than in the Siamese. Different mutations, and hence alleles of a related gene, called *TYRP1*, cause chocolate coloration or albinism.[48]

Like all other genes, *Fgf5*, *TYR*, and *TYRP1* are all coding regions of DNA, in that they code for proteins. But as we saw in the previous

chapter, much of the evolutionary action is in noncoding sequences that regulate the activity of genes. One such noncoding mutation is responsible for the polydactyl condition. The gene that it regulates is one of the most storied in all of developmental biology: *sonic hedgehog* (*shh*).[49] *Sonic hedgehog* is a master developmental regulatory gene that produces a protein molecule of a sort called a "morphogen," which forms a concentration gradient by diffusion.[50] The effects of this morphogen on the cells of the developing embryo depend on its concentration. In this way, *sonic hedgehog* plays an important role in the development of organs, brain, and limbs. Its activity is regulated by noncoding elements near the gene called "cis-regulatory elements." The limb-specific cis-regulatory element is called ZRS. A mutation in ZRS that causes too much *sonic hedgehog* activity is responsible for the polydactyl condition.[51]

The noncoding polydactyly mutation is an example of a genetic mechanism that also underlies several human developmental abnormalities. And this is but one instance in which breeder-induced cat miseries have served to advance human medicine. For many of the ailments of purebred cats, as for purebred dogs, are also found in humans—a legacy of our shared mammalian evolutionary history. Indeed, these medical applications provided much of the original rationale for both the canine and feline genome projects.[52]

Over 250 hereditary diseases of domestic cats are homologous to human diseases. The goal is to identify the genetic substrates for these diseases in cats, and then look for the homologous genetic substrates in humans. Cat models are especially promising with respect to progressive retinal degeneration, cardiomyopathy, and inherited motor neuron disease.[53] The cat may also prove a useful model for amyotrophic lateral sclerosis (ALS).[54] Cats are already important models for several viral diseases, including HIV-AIDS, which is prevalent in free-ranging cats, as is feline leukemia and the feline equivalent of SARS.[55] Research is under way on cats to determine the DNA variants that make some cats more susceptible to these infections.

Until the wildcat genome is sequenced, feline genomics cannot pro-

vide much information about the genetic alterations that facilitated domestication. We can predict, however, that these genetic alterations were more concerned with behavior than with anatomy and physiology. For it is in their behavior that domestic cats most differ from their wild ancestors.

FAR FROM SOLITARY

The vast majority of cats have escaped artificial selection. They are self-domesticated. And except for superficial changes in their coats, domestic cats very closely resemble wildcats. So close is this resemblance, in fact, that wildcats don't make a distinction when it comes to mating. Wherever wildcats—of any subspecies—live in close proximity to feral domestic cats, the two interbreed freely, much more so than wolves and domestic dogs do. This interbreeding threatens extinction by hybridization for several populations of European wildcats (*Felis silvestris silvestris*), notably the Scottish wildcat and the Iberian wildcat.

There is one way to distinguish wildcats from domestic cats without resorting to genetic testing, and that is by their behavior. Even the most feral domestic cats are much more social than wildcats. Wildcats are indeed solitary creatures, with exclusive home ranges. Domestic cats are social creatures, which, in the feral state, often form colonies when food is relatively abundant and localized.[56] When food is less abundant and dispersed, feral cats still interact much more than wildcats.[57] When living in colonies, female feral cats engage in mutual and reciprocal care; they often suckle and protect the young of other colony females, much as lions—the most social of cats—do. Members of a colony also defend their mutual territory against outsiders—again, much as lions do.[58]

Moreover, domestic cats have evolved a novel behavioral signal called "tail up," which they use to signal friendly intentions.[59] This behavior is entirely absent in the much less social wildcats. Lions, however, use the

tail-up behavior in the same way as domestic cats.[60] This is a case of convergent evolution, but the shared ancestry of lions and domestic cats may well render this convergence more probable—a part of the felid behavioral repertoire to which only the most social felids have evolutionary access. Put another way, the genetic alteration required for tail up may be minimal—another example of the conservative creativity of evolution.

It has been proposed that neoteny is at work in the sociability of domestic cats.[61] Meowing, purring, and kneading are all kittenish traits retained by adult domestic cats but not adult wildcats. While kneading may just be a nonadaptive (selectively neutral) by-product of infantilization, the purr and meow are important social signals. There is also evidence that the acoustic properties of the cat's meow have been altered to be more audible to the human ear.[62] (If so, Sylvester—whose meow is rather loud and grating—is much better adapted than Smoke, whose meow retains a kittenish volume and softness.) We could even say that Sylvester is in the vanguard of cat evolution.[63]

The domestic cat certainly lends support to Belyaev's hypothesis that in the domestication process, behavioral modifications for tameness come first, physical changes only later. For domestic cats remain only superficially dissimilar to their wild ancestors. In the fox experiment, tameness came by way of intense artificial selection; for the wolf, and especially the wildcat, tameness came by way of natural selection in a human-created environment. For the wildcats, unlike the wolves, there was an additional psychological barrier to overcome: the close proximity of other wildcats, which were congregating around the granaries. Only these more social wildcats, those who were the least stressed by the close proximity of other wildcats, could fully exploit this new resource.

These social wildcats, upon further selection to tolerate humans, were then ready to include us in their social circle. For all of their celebrated independence, cats don't just tolerate us; they enjoy our company. Smoke is asleep on my printer; Sylvester is back on my lap.

CATS IN A DOG WORLD

Human attitudes toward our domesticated animals vary greatly over time and culture. We saw this with dogs, which have been eaten, petted, or ignored, depending on time and place. Indeed, while dogs are taboo foods throughout most of the world today, they are still consumed with gusto in China, Korea, Vietnam, and Polynesia. But, with the notable exception of Islamic cultures, dogs are generally not viewed as unclean, unholy, or otherwise deserving of opprobrium. On average, across human history and cultures, dogs evoke neutral to positive emotional responses. They rank just below horses in positive regard.

Notwithstanding their deification in ancient Egypt, cats are viewed much more ambivalently, though again with great variation over time and space. In western Asia the cat was long associated with female sexuality and fertility, attitudes also found in much of pagan Europe. The spread of Christianity was bad for cats, perhaps as a result of their association with pagan religions; they came to be viewed as the devil's agents and closely associated with witchcraft. During the Middle Ages feast days were particularly dangerous for domestic cats; they were tortured in the most gruesome fashion: boiled or burned alive, slowly roasted on spits, flayed, and maimed. There was a strong current of misogyny in this cat hatred, as in the persecution of putative witches. Fortunately, things have improved for cats since. In our more enlightened age, stray cats are often cared for or adopted. Cats are the most popular pets in the world today.

Yet cats are still viewed much more negatively than dogs, according to a recent survey of Americans. Some cat haters can't abide feline independence; some no doubt are still spooked by hoary associations with witchcraft and paganism generally; and some just see dogs as the paragon of companion animals, by which standard cats are deficient. Dogs are an inappropriate standard by which to measure the merits of cats, yet many persist in this mistaken belief. It was recently explained to me, by

way of demonstrating the superiority of dogs, that "a cat won't pull you out of a burning building"—the implication being that it is because of a lack of motivation rather than the manifest physical inability of cats to accomplish such. A cat won't put its life on the line like a dog will.

Maybe, maybe not. There is a widely watched Internet video that suggests otherwise. In it, a four-year-old boy is stalked and severely attacked by a mid-sized dog of uncertain pedigree, when, from off camera, a tabby cat streaks across the screen and flings itself at the much larger attacking dog. The dog, not having a clue what hit it, takes off at high speed. Cats, it seems, can be just as heroic as dogs.