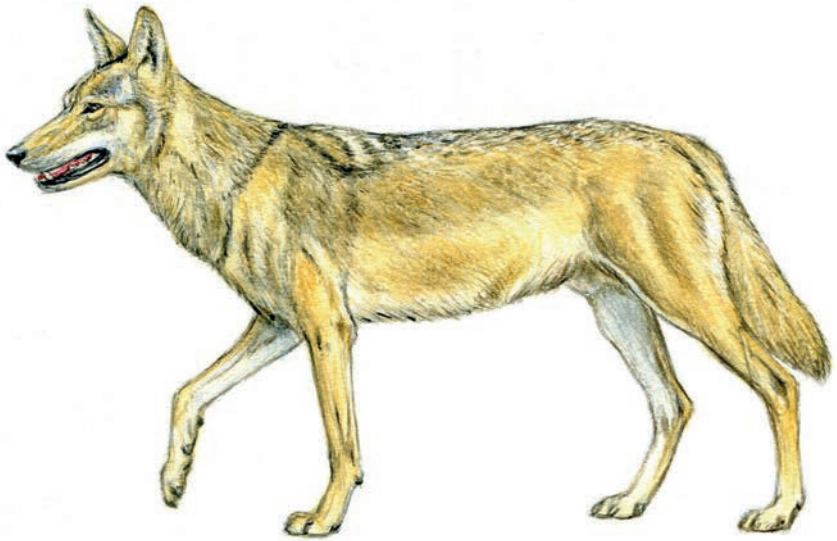
CONTENTS

Wolves, the largest wild canids in the world, live mostly north of 20° N latitude. They vary greatly in size; on a south–north gradient (known as a cline), the larger wolves are in the north. The largest subspecies in North America are the northwest and arctic wolf; the smallest are in the desert southwest, in Mexico, and in coastal British Columbia. In Eurasia, the largest wolves are in Russia and Fennoscandia (Norway, Sweden, Finland, and Russia's Kola Peninsula) and look similar to the northern North American wolves—probably because of their shared evolutionary history (wolves migrated from North America through the area that is modern-day Russia) and the fact that they inhabit northerly latitudes. The Iberian, Italian, Persian and Indian wolves range between medium and small in size.

BUILT TO HUNT

In many mammalian species the male is larger than the female, and this is true of gray wolves—fully grown males are approximately 20 percent larger than females. A primary reason for this is the competition for mates between males, although this is not the case with wolves. Wolves are mostly monogamous, which doesn't mean there isn't mate competition, just that the selection pressure for large males due to male–male competition is less. The size difference between male and female is likely due to a division of labor in terms of hunting tactics: females' smaller size is better suited to chasing prey, whereas males are larger and stronger for the takedown. Males' size is also a key factor in territorial battles. A mature wolf may be 6.5 ft (2 m) in length, including the tail, and stand 3.3 ft (1 m) at the shoulder—about the size of a German shepherd dog. A wolf's weight ranges from 66 to 110 lbs (20–50 kg) for females and 88 to 148 lbs (40–65 kg) for males, and it varies seasonally. All wolves live in a seasonal climate (as opposed to a wet-and-dry-season climate) and typically weigh more during winter, a time of year when they generally consume more food due to



INDIAN WOLF
Canis lupus pallipes *is a slightly built wolf with less underfur, and is smaller than the Eurasian wolf. It ranges across the Middle East to India.*

greater prey vulnerability (see pages 137–41). After someone has encountered a wolf in the wild, it's not uncommon for them to overestimate its size. I have frequently heard people describe seeing a wolf they say was at least 180 to 190 lbs (82–86 kg). Of the more than 500 individuals we caught in Yellowstone, the largest was 153 lbs (69 kg), and he likely had food weight in his belly. He was an outlier: most of the mature males among those 500 weighed around 115 lbs (52 kg), with the females usually below 100 lbs (45 kg).

Bulking up

At around 5–6 years, the typical life span of a wolf is relatively short. A consequence of this is that wolves achieve maximum size quickly: peak skeletal dimensions are achieved by males and females after 6–8 months, whereas for other mammals this can take more than a year or longer. It takes longer for them to reach peak weight; females attain maximum weight after 1.8 years, while males

continue to add weight until about five years of age. This change in male size is noticeable and impressive. Having watched numerous wolves grow from a pup to an adult in the field, then catching and handling them, I at times felt I was not holding the head of a wolf in my lap, but rather a basketball, the head was that massive. A male wolf will gain most of its weight in the third year of its life, with the rate of increase slower for the remaining two years. Females maintain their weight, or continue to add weight throughout life, albeit at a slower rate. Males, on the other hand, will lose weight after achieving their maximum size. The reason for this is unknown, but it likely relates to the energy required to maintain more muscle mass and larger body size. It is a common symptom of the aging process in many mammals, including humans. These differences between sexes likely suggest different selection pressures, with female development adapted for reproduction, and males for hunting and territorial defense.

In addition to developmental factors specific to the species, a wolf's weight will change depending on how much food it has to eat. The availability of prey varies seasonally and across years. Wolves are adapted for a "boom and bust" feeding style, as prey are typically difficult to locate, and once located, difficult to kill. As mentioned in chapter 1, the prey that wolves target are often significantly larger than themselves, and they are by no means guaranteed to succeed. When they are able to feed, they will take in a lot of calories (the stomach capacity of a wolf is 22 lbs [10 kg]), providing them with the reserves to survive extended periods without food.

Wolves need to consume 7–8 lbs (3–4 kg) of meat per day to survive, and they will typically go several days between meals. In one instance, a wolf survived 117 days without a meal, which is a remarkable feat. If they find or receive (in the case of experiments) food again, they have the ability to regain lost weight quickly, usually within a couple of days. When wolves eat a fresh kill, the organs are consumed first. To wolves, this is the most appealing meat with the highest nutritional value. Organ meat is very high in fats, which are highly prized by wolves.

Do wolves fight over these juicy parts? Many accounts of wolves have them snarling and competing over the spoils of a fresh kill, and plenty of photo-

graphs have captured this type of behavior. Some work on captive wolves suggests that the dominance hierarchy is enforced while feeding on kills, with the most dominant wolves feeding first and the subordinate wolves having to wait. This does not appear to be the case in the wild, where wolves have been observed feeding in a calm manner, with relations between the pack members appearing amicable. Often, the wolves that made the kill do not feed first. It has even been recorded that the top-ranking female in the pack came in and took food from a male wolf that had made the kill!

Adaptations of a carnivore

The wolf's skull anatomy reveals adaptations characteristic of a generalized carnivore. Longer than that of other carnivores, to allow for maximal jaw opening, it is robust and designed for the takedown of large prey. A long rostrum (nose) allows for a large olfactory organ, which equips wolves with a strong sense of smell—a key capability when finding prey and scavenging carrion. They can follow scent trails of other wolves for miles. They use their powerful legs to cover long distances in search of prey, and keen senses—in addition to exceptional

BUILT FOR SMELLING
The elongated skull houses olfactory apparatus that wolves rely on when hunting—in contrast to cats, which are more visual hunters.

UNFORGETTABLE EYES
Wolves will often scan great distances across largely unobstructed landscapes in search of prey, something to which their round pupils are well suited. Look into the eyes of a wolf, and you'll never be the same.

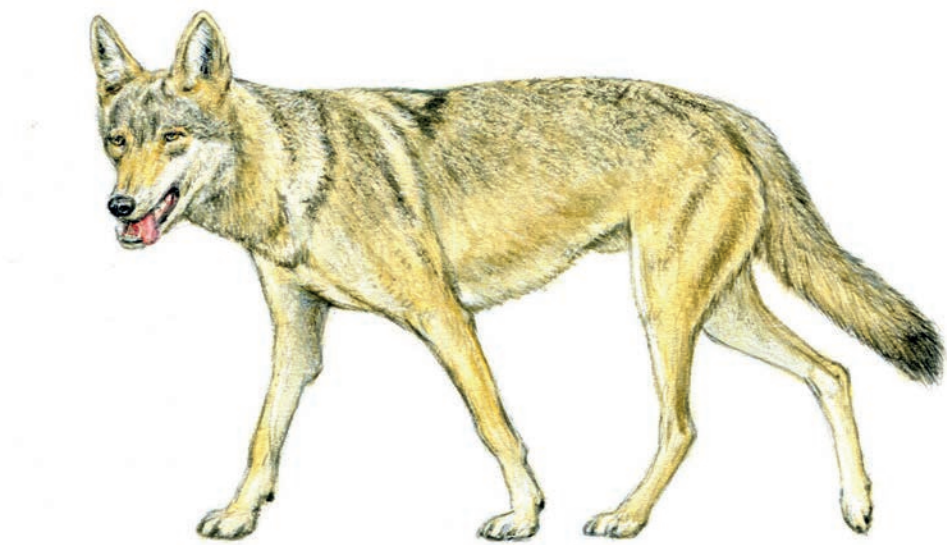
smell, they have sharp vision and acute hearing—to locate it. Their strong jaws and specialized teeth are ideally suited to seizing, killing, and consuming it. Throw in some social and competitive adaptations and that, in sum, is a wolf.

Interestingly, wolves have round pupils—unlike some cats and foxes, which have elongated pupils. Elongated pupils are more common in predators that are short and can't see above obstructions at close range and need to stalk or ambush prey, as this gives them better depth perception. When pursuing a potential meal in typically more confined spaces—through dense vegetation, for example—they must be able to gauge its proximity effectively and quickly, assess distance, and select the optimal moment to strike. In contrast, wolves will often pursue a target across open terrain, for which another set of visual capabilities are better suited.

DENTITION

Fed by its teeth

A Russian proverb says that the wolf is fed by its feet. The feet are undoubtedly important, but the teeth must do the killing, without which there is no meal. Firmly rooted in the skull are an impressive array of 42 teeth: 22 in the lower jaw and 20 in the upper. With two sets, milk teeth and permanent (the latter in place by about seven months of age), these tools are key to a wolf's survival. Their teeth take a considerable beating. The task of bringing down large prey takes its toll, and a wolf's teeth often become worn and can even break. Wolves—and mammals in general—seem to know this, and they are careful with their teeth, refraining from using maximum bite force due to the chance



ARABIAN WOLF
Confined to the Arabian Peninsula, Canis lupus arabs *is a long-legged, small, thin wolf with sparser fur except along its back, which likely offers protection from sun.*

of biting something hard, such as a bone. This is in contrast to reptiles, which grow more than two sets of teeth, enabling the replacement of damaged teeth. Thus, examining tooth wear and breakage is a good way for scientists to estimate the age of a wolf.

The importance of the teeth is due to the oversized role they play in immobilizing and killing prey. Wolves do not have supinating forearms and paws, which enables other animals, such as cats, to rotate their forelimbs upward—a feature that aids them in climbing. A wolf's claws, unlike those of a cat, aren't retractable; they remain out the whole time, getting worn down by travel. This combination of restricted movement of the forelimbs and dulled claws means that the teeth have to do most of the work bringing down prey. This is best exemplified by comparing cross sections of cat and wolf canines. The latter

DENTITION

The lack of flattened tooth surfaces among its 42 teeth reflect the wolf's meso-carnivorous diet. Rather than grinding and crushing its food, wolves use their teeth to seize and hold onto prey, and eventually to tear chunks of flesh from it.

have an elliptical shape that is strong along the length of the tooth, front to rear, whereas the former are rounded. Cats typically pounce on top of prey and bury their teeth deep into flesh, quickly subduing it—an action that doesn't generate much torque. Wolves, on the other hand, attack from below while on the run, grabbing where they can and hanging on, often getting dragged along, which really strains the teeth. I have seen wolves lock onto the neck of an elk and get dragged for tens of meters, and in one case even get slammed against a log, which did not dislodge the wolf. Tooth strength here has to be substantial, and such extremely arduous hunting events as these explains why most old wolves have broken teeth (not to mention broken ribs!). I have tried to remove canine teeth from a dead wolf and not succeeded, even when using a tooth elevator and pliers.

Multifunctional

In addition to taking down prey, wolf teeth are designed for grabbing, cutting, and shearing. A consequence of the wolf's long snout—needed to accommodate all those teeth—is reduced bite force. The longer snout distributes force across the jaw and away from the hinge point, dissipating strength, whereas a shorter jaw would concentrate force and allow for more compact muscles. The canines, critical for seizing and killing prey, are positioned far forward in the jaw, which limits the leverage the wolf can employ and therefore their power. The long snout is likely an evolutionary trade-off: what the wolf loses in bite force, it gains in smell and speed (a longer jaw closes faster), with the skull shape housing an advanced olfactory system. The canines and incisors are well suited to tearing out bite-sized chunks of meat for easy swallowing, a process called mechanical digestion. None of a wolf's molars are flattened, which is typical of teeth designed for greater mastication before ingestion, as in bears and humans. A wolf's method of eating, in which it gulps its food down without chewing, makes it vulnerable to swallowing harmful objects. Some people take advantage of this fact to kill wolves, placing nails or razor blades in chunks of meat, which are swallowed whole by the unwitting animals. Once through the mouth, the food is swallowed and undergoes chemical digestion.

EFFECTIVE TOOLKIT
A common feeding position, wolves use their powerful carnassial teeth, last upper premolar, and lower first molar to shear and cut meat, and even bone, from a carcass.

The anatomy of a bite

Wolves have a total of 12 incisors (three on each side of the upper and lower jaws), four canines (one on each side, top and bottom), 16 premolars (four on each side, top and bottom), and ten molars (two on each side at the top and three on each side at the bottom). A crest on top of the skull (the sagittal crest) and a broad arch on the side of the skull (the zygomatic arch) provide attachment for large masseter muscles that are used to move the jaws and inflict potent bites, as well as other jaw muscles that act sequentially from back to front, for greater strength. The jaw opens widely via a single joint, which helps to prevent it from dislocating.

The incisors are suited to finer operations, such as cleaning flesh from bones, and are used dexterously by wolves. They are arranged in a slight curve, allow-

ing for a broader range of functions—a feature that is thought to be a basic carnivore adaptation to omnivory, as wolves sometimes consume food other than meat. In her classic book *Arctic Wild*, the writer and conservationist Lois Crisler described lying down with her captive Alaskan wolves, closing her eyes, and having one of them carefully groom her eyelids with its incisors: "like a row of needles [the wolf] was picking up the merest skin of my eyelid with her teeth, giving me grooming nibbles." Since reading this I have always been jealous of Crisler. I too hand-reared wolf pups for research, slept with them, and bottle-fed them, but they never groomed my eyelids. Lastly are the wedge-shaped molars and premolars, including the carnassials—the upper fourth premolar and first lower molar. Unique to carnivores, the carnassials serve multiple functions. As well as being the ultimate shearing and cutting tools, they are strong enough to crush bone, an action that is particularly harmful to teeth. Working together, the carnassials can cut, shear, or break just about anything.

I have examined these teeth on my dog and a sedated wolf. I got nervous on the wolf, even though it was sedated. Just putting my finger in there hurt, giving me a twinge of pain and a desire to quickly pull my finger out!

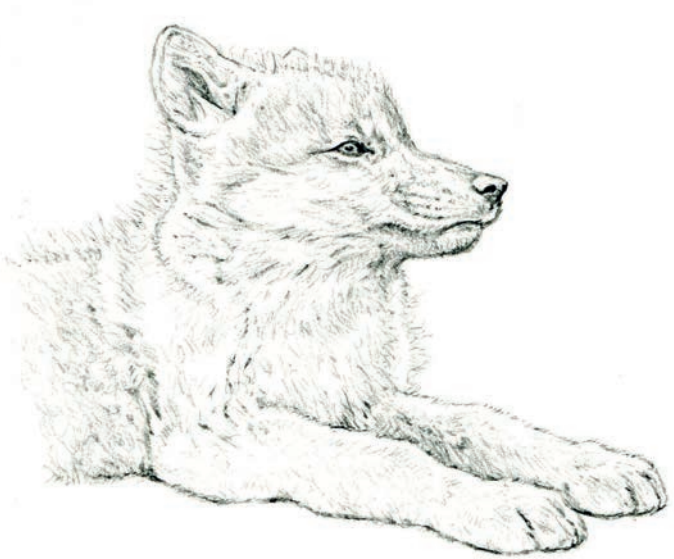
Wolves frequently gnaw bones. Bone chewing is more common among wolves when food is scarce and competition high—a behavior that leaves its mark on the wolves' teeth, and presents scientists with a productive area of study. Blaire Van Valkenburgh, a paleontologist at UCLA, studies tooth breakage in carnivores. She has used tooth breakage patterns from wolves in Yellowstone and Isle Royale, Michigan, to correlate tooth breakage with food consumption, finding greater breakage when food is scarce in both places. She also examined tooth breakage in fossilized carnivores, finding greater tooth breakage when more species were present in the fossil record, suggesting more competition and the greater need to more fully consume food items. A canine dentist would have made a killing in the Pleistocene!

These feet are made for walking

As with their teeth, so too with the rest of a wolf's anatomy: its specialization for hunting extends beyond its dentition. A wolf must cover large distances in search

of prey, so their bodies are built for endurance. Limited rotation at the hips and elbows increases running efficiency, though at the cost of reduced maneuverability. Because of the risk inherent in hunting things larger than themselves, wolves must be highly selective when choosing their prey. This includes finding animals that are vulnerable, whether that's injured white-tailed deer struggling to survive the winter, or an elk calf left temporarily alone while its mother forages for food. To do this necessitates encountering a lot of potential prey, likely across a vast stretch of land. From an evolutionary standpoint, it's unsurprising that adaptations have endured that favor long-distance mobility over agility. They're perfect for a cursorial existence—one that is adapted for trotting or running.

The emergence of cursorial wolves reflects environmental changes across their range. Their increasing mobility coincided with climatic changes that led to drier, more open grassland habitats, which helped them to travel farther. What's more, an important anatomical change in the foot played an important part. Over time the heels of wolves' feet lifted up, so they walked on their digits,



BAD HAIR DAY
Although probably not a scientific identifier, pups at a distance can be identified by the long guard hairs standing erect on their back, almost like a perpetual "bad hair day."

not on the soles of their feet. This type of walking is called digitigrade, as opposed to plantigrade, which is walking with the heel touching the ground.

These adaptations allowed wolves to move around very capably, and their endurance is especially notable. Their muscles are fatigue-resistant: increased blood flow to the muscles allows wolves to maintain intermediate speeds for long periods of time. Wolves can trot at roughly 3–6 mph (4–9 km/hr) for hours on end, meaning they can travel for tens of miles per day. Top bursts of speed are another story, as wolves are not as fast as some other carnivores over short distances. They can reach speeds of only about 35–44 mph (55–70 kph).

Cold-weather creatures

Lastly, wolves are better adapted to cold than heat. A big part of their evolutionary history was spent in the north, above the glaciers, before extending down into more southerly climes. Although they eventually reached low latitudes, they are much more susceptible to heat stress than cold. Reintroduction projects always transport wolves in winter months and not summer. While it can get too hot for them, it can never get too cold.

Part of this is due to the fact that their fur (or pelage) is supremely adapted to keeping out the cold. As with many mammals, their fur comprises two layers that work to trap air for insulation. The underfur traps the air and is protected by guard hairs, which shed moisture to keep the underfur dry. Across the shoulders the guard hairs are exceptionally long, and on pups they often stand up, making it look as if the youngsters are having a perpetual bad hair day. One benefit of this is that it helps researchers to identify pups at a distance in the field.

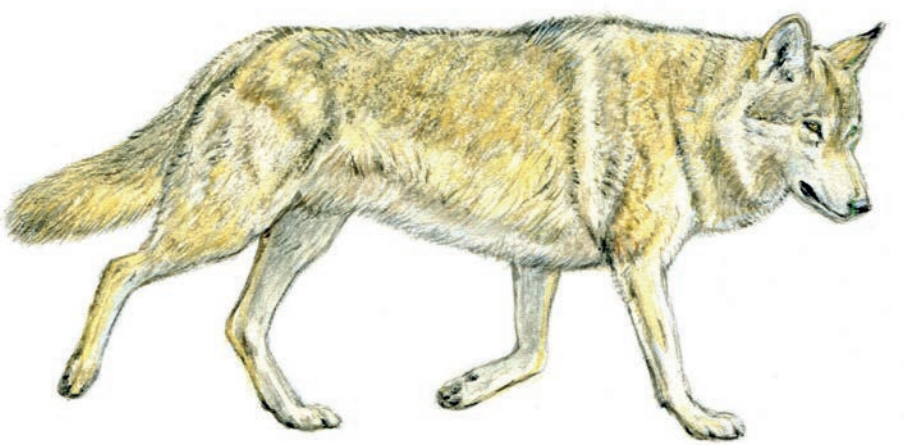
Another key feature of their pelage is the seasonal variation in thickness. The wolf's winter coat is so ample it provides significant extra thickness to their body and necks. This is an issue when fitting a wolf with a radio collar: while it might fit tightly in winter, by spring the wolf has shed enough fur that the collar is prone to slip off. The key, then, to fitting a collar is to gauge the size of the skull, not the thickness of the fur. That said, the collar should never be too tight, and it is best to err on the side of caution.

Coat color

A wolf's habitat requirements are simple: protection from humans and a regular supply of large, hoofed mammals for prey. Fortunately, when it comes to food, a wide range of habitats across the northern hemisphere fit the bill, be they deserts, forests, tundra, or mountains. Although some wolves follow migrating prey, such as the barren-ground caribou in subarctic regions of North America, for the most part populations are resident in one area for the entire year.

As discussed in chapter 1, a number of eco-evolutionary factors have contributed to an increasing genetic similarity between wolf populations across their gigantic range. Nevertheless, there are subtle differences between subspecies. A good example of this is coat color.

There are three basic color types (called morphs)—gray, black, and white—and the color changes as a wolf ages. A gray coat may turn white, and a black wolf may become gray. Gray is the most widespread, occurring across the entire wolf range. It is typically lighter in the north and darker in the south. It is also highly variable, coming in all kinds of colorations. Black occurs mostly in mountainous



TIBETAN AND HIMALAYAN WOLF
Canis lupus chanco *has been neglected, to the extent that its population status is unknown. It carries unique genes and is deserving of increased research attention, as well as greater protection.*

habitats, typically those with lush forests, such as the North American Rocky Mountains, and in Italy, India, and Iran, while white is found mostly at high latitudes. These are general trends; occasionally, white wolves pop up farther south, and black wolves occur outside of the Rocky Mountains (more on that later).

For a long while, it was thought that the different color morphs served primarily as camouflage, but as we'll see later on, this theory was eventually turned on its head. Either way, a wolf's coat color does help it to blend into the surroundings, and this is especially true of gray. The coats of gray morph wolves contain an almost infinite number of patterns and tonal combinations, from brownish and blackish to mostly whitish. While some subspecies are identifiable by their coat color—Mexican wolves, for example, exhibit a distinctive gray tone—the overall effect is of concealment. Try spotting a gray-colored wolf on a late fall day with little green vegetation and maybe a patch or two of snow here and there. The wolf could be near enough right in front of you and you would have a hard time seeing it. That is how well gray can blend in. Wolves with gray coats don't really stand out on a snowy landscape either, whereas black wolves do—at least until you get into the forest, where a black form on snow amidst trees can be hard to spot. Forests at all times of the year are dark.

Pulling hairs

Another interesting thing about gray coat morph is the banding patterns of each individual hair. If you pull a hair on a dog, you'll notice this. One time in Yellowstone, we were holding an unknown species of canid in a pen that had been captured by a rancher in Wyoming by running over it several times with a snowmobile (a horrific practice which I'll write about later). This was important because preliminary surveys had found no wolves in the Yellowstone area. They had been extirpated, which means they had become locally extinct. Although it didn't really look like a wolf, it did bear some similarities to one. This was the mid-1990s, when genetic techniques were not advanced enough to be able to determine whether it was a pure wolf. The canid was sent to Yellowstone to hold in a pen until we could figure out what it was. After working with wolves for a few decades, one gets an intuitive feel, or "gestalt," for identi-

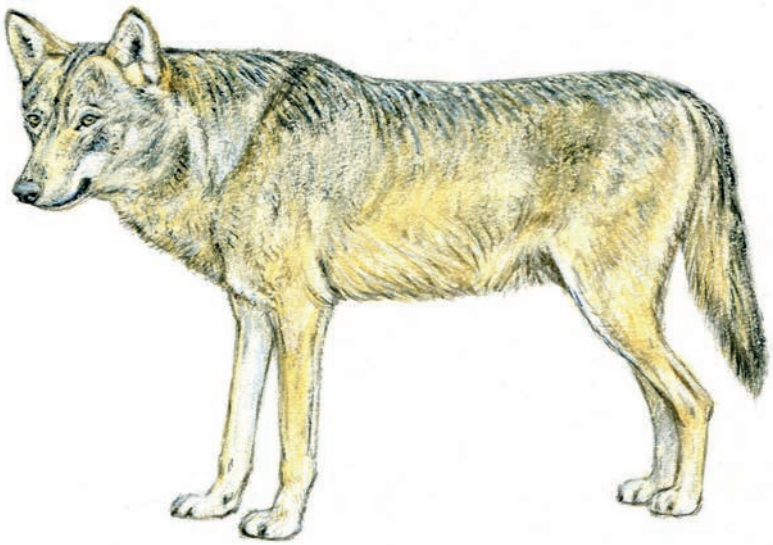
fying wolves. As I say, this particular canid definitely had wolflike traits, but notably it didn't act like a wolf. It seemed a little odd and was standoffish but not wary—in a creepy kind of way—and I have been around my fair share of wolves in pens. My very first wolf job was with a captive pack of wolves, and I went into the pen with them frequently. They were most definitely wary of me. We needed to draw blood from it for genetic analysis, but also to pull hair from its coat, because genetic analysis isn't always definitive (back then at least).

Hair in canids exhibits species-specific banding patterns. In this case, the canid had a hair banding pattern similar to a dog, not the banding pattern of a wolf. Thus we concluded that our mysterious newcomer was not a wolf, and that there were no wolves in our release area. This was likely a wolf–dog hybrid that had either escaped or been deliberately released. It was clearly not tame, but also not unfamiliar with humans. It lived out its life in captivity—fortunately we were able to find a zoo that was willing to take it.

Black wolves

As I started my first job with wolves, at a captive facility in Indiana, I hadn't thought much about their coat color. I had assumed that wolves were mostly gray. My next two jobs did little to correct that misconception, given that they were in the Great Lakes region of the USA, in Michigan and Minnesota—a region where there were not many black or white wolves. My understanding about coat color changed after I landed in Yellowstone, where my job was to reintroduce wolves from western Canada to Yellowstone. Of 41 wolves reintroduced, 25 were gray and 16 were black.

Black coat color in wolves has a long history, and it doesn't actually originate from wolves, but rather from dogs. Dogs are the descendants of wolves, and emerged 15,000–60,000 years ago. It was in dog populations that the black coat color first emerged, after which interbreeding between dogs and wolves passed the black coat color from the former to the latter. It is hypothesized that this exchange of genes occurred somewhere in northwestern North America, in the region of the Yukon and Northwest Territories, 1,600–7,200 years ago. Black wolves are most common in western North America, and are relatively



ITALIAN WOLF
The distribution of Canis lupus italicus *is restricted to central Italy and the French and Swiss alps. The wolf is medium-sized with a compact body and darker tones to the fur.*

rare everywhere else. This rarity is likely due to other reasons (see page 56). Where the black coat color does occur in the Old World, for example in Italy, hybridization with dogs is the likely cause.

This black coat color proved to be very beneficial for wolves, and the evolutionary advantage it conveyed ensured its continued selection. But the reason for this was not what I initially suspected. Since black wolves are most common in the forests of the Rocky Mountains—and I often had trouble spotting them there—it made perfect sense to me that their coat color offered an advantage to them in that environment. That is, until researchers conducted genetic studies of black coats, and drew some fascinating conclusions.

Different pairs

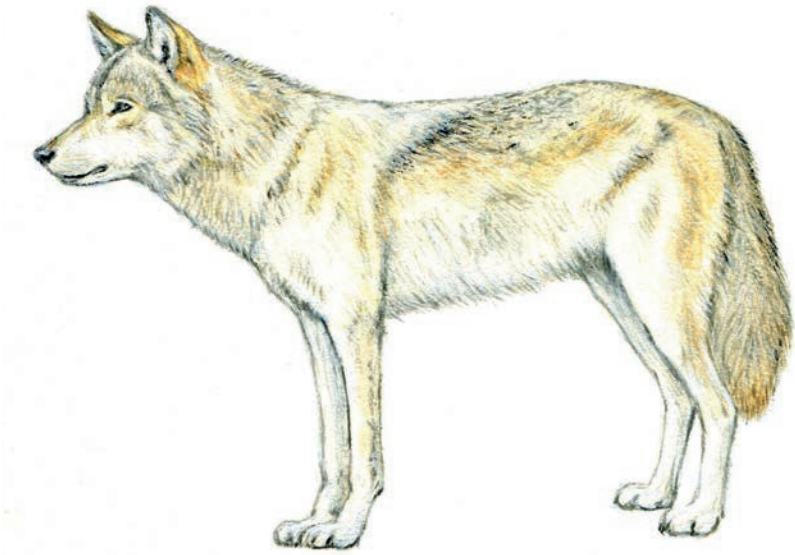
To understand what advantages the black color affords, we have to take a look in more detail at genetics. The genes for black coat color are located on the

chromosome at a site called the K locus, which also regulates production of a protein that aids immunity against disease in mammals. Canine distemper virus is particularly harmful and can kill a lot of wolves, especially pups. In a stroke of evolutionary luck, having a black coat can reduce a wolf's susceptibility to canine distemper, and could therefore reduce mortality among black wolves.

The benefit only comes in the heterozygous condition, where the black wolf has one black allele and one gray. Alleles are two options for a trait—in this case a black or gray coat, where black is dominant to gray and so is the only one to be expressed, while the gray allele is hidden. This is important because it can appear in later generations. The presence of two black alleles (called homozygous) would also produce a black coat color, but without giving the wolf enhanced immunity. The reason for this is unknown.

This is important, so to better understand this, let me back up a step. At a given location on a gene there are two versions for a particular trait—in this case gray or black coat color. Through sexual reproduction, one of these two choices from each parent is randomly selected, leading to three possibilities for their offspring: gray/black, black/black, and gray/gray. As black is dominant over gray, the first two combinations will appear as black wolves, and only gray/gray will appear as gray. The immunity benefit only comes in the heterozygote, or gray/black form. In fact, only 5 percent of black wolves in Yellowstone are homozygous black. Black wolves are not more common than gray wolves, despite more wolves being born with black coats, because wolves with two black alleles have a lower chance of survival. For example, in Yellowstone the proportion of black wolves to gray wolves over 30 years has stayed more or less at 1:1.

Talk about delving into the details of life. Discoveries like this are so fascinating that one wonders how many other aspects of life have secrets like this. What is clear is that it is only possible to make such discoveries through long-term collaborative research. Most scientific research lasts between 3 and 5 years, which is roughly the length of time for a graduate student to complete their degree. But unraveling deep, complex secrets takes years of work and involves many brilliant minds across various areas of expertise. It is really hard to do this! Funding is

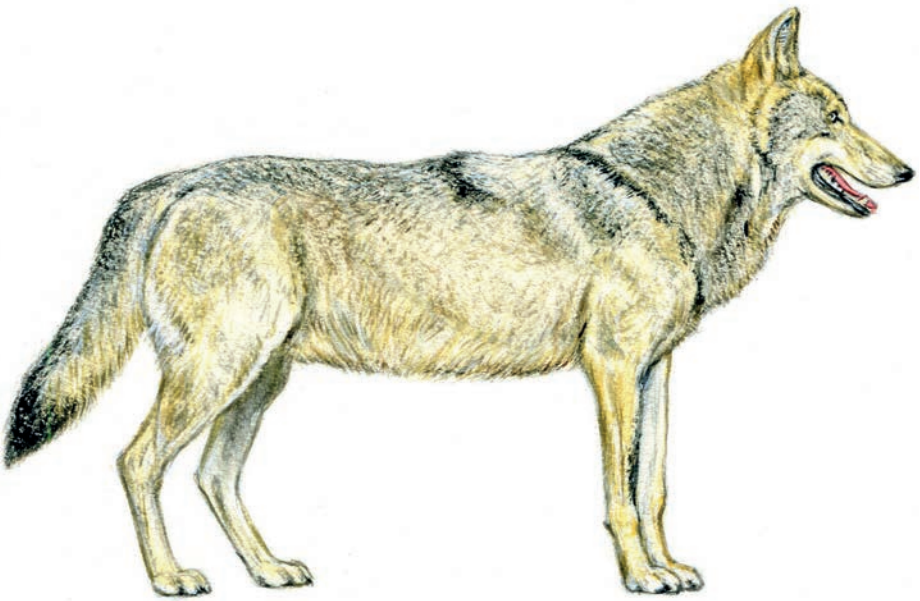


TUNDRA WOLF
As its common name suggests, Canis lupus albus *is mostly a tundra subspecies, hence its large size and robust frame adapted to northern climes.*

usually ephemeral, and nowadays people rarely hang around long enough at one job to see through many years of cumulative research.

These findings do not support my former assumption, which has no doubt been held by many others, that the variation in wolf coat color is related to camouflage. It is yet another example of the value in establishing truth by finding things out, rather than supposing things to be true. Mark Twain, arguably the greatest American writer, once said, "Supposing is good, but finding out is better"—which pretty much sums up the value of science to society.

Amazingly, this is not the end of the black coat color story. Given that black coat color changes across North America, and black wolves have a higher resistance to some diseases, maybe data about disease outbreaks and their frequency might help to explain the distribution of black coat color in wolves. We set out to test this by collecting blood samples from wolves all over North America and checking for their exposure to distemper (plus the frequency of outbreaks).



IBERIAN WOLF
With a range limited to the Iberian Peninsula, Canis lupus signatus *is somewhat genetically distinct. Reduced to small populations, numbers have recently increased—they are often present in agricultural areas and will utilize carrion.*

We found that the incidence of black coat color is indeed related to the frequency of distemper outbreaks, establishing that the population of black wolves increased as the frequency of distemper outbreaks rose. This can be explained by the immunity advantage conferred from the heterozygote (black/gray) coat color. We compared the incidence of black coat color and the frequency of distemper and found a clear correlation: in periods of fewer distemper outbreaks, black wolves were relatively uncommon.

Opposites attract

It's a familiar saying, but is it actually true? For wolves, the answer appears to be yes. The fitness benefit of black coat color only comes in the heterozygous,

or black/gray, condition, which would require a mating pair consisting of a black and a gray wolf. Astonishingly, this configuration was what we found in Yellowstone—most wolf pairings comprised a black and a gray wolf. There were fewer than predicted gray/gray pairings, and only a couple of packs that contained only gray wolves. Through modeling—a mathematical process that involves taking real-world data and creating different scenarios—it was shown that black coat color would disappear if distemper outbreaks were not frequent enough, which helps explain the coloration of wolves across North America. At this point, I must confess that while we were assembling this research and writing the scientific papers, a whole series of questions arose: How do the wolves know who to mate with? What is the mechanism by which a wolf in the field during the breeding season identifies the mate that will give them healthy, resilient offspring? No one had an answer. However it works, the phenomenon is called negative assortative mating, or disassortative mating (both are mouthfuls, for sure), and it is exceedingly rare in the animal world—at least, as far as scientists have been able to ascertain. Wolves are the only mammals that mate in this way. It is likely that the disease immunity conferred by negative assortative mating is key to explaining the behavior.

Gray area

Studies of wolves with gray coats have thrown up some interesting results. For example, research in Yellowstone established that females with gray coat color had 25 percent higher annual litter survival than females with black coat color. It's hard to know why this is, but one theory posits that heterozygous black coat color imposes a cost, to go along with the documented health benefits, such that there is higher mortality among heterozygous black pups. The precise nature of that genetic downside is yet to be established, but the phenomenon has been documented in birds and other mammals, so there is at least precedent. Another area of interest centers on behavior. Work carried out by Kira Cassidy, a researcher in Yellowstone, together with other scientists, found that wolves with gray coats are more aggressive when packs clash. When packs engage in territorial battles—wolf turf wars—gray wolves are more likely to

chase rival pack members compared to black wolves. This runs counter to what we might expect to see, because it's considered more common in nature for darker animals to be more aggressive. The team found that gray-coated wolves had higher levels of the stress hormone cortisol than black wolves. This is mirrored in dogs—black dogs have lower levels of cortisol and are less aggressive. The research poses a number of intriguing questions. For example, is there a cost associated with greater cortisol production? Does it impact gray wolf immunity to certain diseases? Everything in life is a trade-off: getting more of one thing will often mean getting less of another. Being heterozygous black confers immunity advantages to disease, but maybe at a cost of being more docile, which lowers survival against more aggressive gray wolves. In which case, we end up with roughly equal numbers of black and gray wolves.

This attests to how much of life is hidden, and coat color is a good example of that. It also shows how little things lead to big things, especially when lots of time is involved. Studying wolves across the world for many years allows us to slowly unravel the mysteries of wolf biology.

3

A WOLF'S LIFE

HUNGER DRIVES

A wolf pack's year can be divided into two periods: pup-rearing, when they remain near the den while the pups mature, and nomadic, when the pack travels more freely. The timing of each is determined by food availability.

Winter bounty

Generally speaking, prey are easier to kill in winter because the demands of the season weaken them. Their favored plants are not growing and the food that is available is less nutritious. In winter, vegetation contains 3–4 percent protein, whereas a growing plant will have 12–14 percent protein content. What's more, moving around in search of food—frequently through deep or crusted snow—is more challenging for prey during the colder months and so requires more energy. The food is often buried, too, making the job of finding a meal even harder. All of this results in prey animals eating less and being in poorer condition in winter, making them more vulnerable to wolf predation because they are easier to kill. Wolves end up eating more, and are primed to reproduce. This is why the wolf breeding cycle begins in late winter.

For females, late winter is a great time to begin a family. Unlike many other carnivores, which do not have an annual or seasonal breeding cycle, wolves usually breed every winter.

Wolf packs do miss years, though, and scientists are still working out what that means. Often it's due to the untimely death of a breeder just before the breeding season, when there is not enough time for a replacement to be found, although there can be other reasons, too. In some populations, over 90 percent of the packs will reproduce in any given year; in other populations, that number may be as low as 70 percent. The difference can probably be explained by whether the wolves are part of a colonizing or saturated population.

In general, the wolves in colonizing populations have access to more prey, eat better, and therefore produce more pups, and they exist at lower densities. A saturated population exists at higher densities and is in greater equilibrium

EARLY TO BREED
Wolves become sexually mature at a young age, and they are highly productive, breeding once a year and typically producing large litters.

with its prey, making food less abundant and so reducing reproductive output. This is referred to as habitat saturation, and it triggers an almost universal rule of nature: density dependence. This is when individuals perform less well, ultimately affecting the population because it has become large enough that resources are limiting. Early on, in a colonizing population, resources are generally not limiting, population growth is high, and there is less competition and no density dependence. When wolf numbers increase sufficiently, the wolves will compete with each other for food and space. Unlike in the physical sciences, biology has very few laws—some would say none—but density dependence comes closest to being a biological law, along with evolution via natural selection.

Starting a pack

A winter of plenty leads to pups being born in spring, when females are in the best yearly condition. The arrival of offspring changes a wolf pack's way of

living. "Pack" is synonymous with "family" because most packs are a family unit, although that is not the case with all of them. I'll discuss this in more detail later. I call the pups the "ball and chain," as once pups are born the pack's activities must center on the den, which is where the pups are usually born. With pups, a pack's activity is structured like spokes on a wheel, with the den at the center and adult wolves traveling to and from the den. The pups ensure that life will revolve around them, at least for a time.

Mating season takes place in mid-winter, and it can be a stressful time for wolves. It represents a big chance each year to improve their social position by starting a pack of their own and passing on their genes, which is life's ultimate goal. Much of an individual wolf's year is spent preparing for the breeding season. No wolf is more important than the lead female; she is the most dominant female in the pack and much hinges on what she does. For one, she usually selects who to breed with, and typically that is the most dominant male in the pack—the alpha male. The scientific literature refers to this as female choice, and it governs a lot of animal life. It's not immediately obvious because the males are often bigger and appear behaviorally dominant, so are assumed to be in charge, and at times they fight for access to females. Female behavior is less overt and more subtle, and it can easily be missed by a scientific observer. What's clear is she's not going to breed with a male she hasn't picked, and she doesn't always choose the most dominant male. It's up to her, and breeding with a lower-ranking male has been recorded.

Once the female has selected her mate, the male guards the female against intruders or "sneaky" males and cheaters (see page 66). Typically, I catch and collar wolves in winter by helicopter, and the noise and spectacle are stressful for them. From my vantage point in the air, I can spot the breeding pair in seconds, because the wolves run every which way, except for one—he sticks with his gal. That's the breeding male with his mate. I usually go for them as it's good to have collars on the breeding pair.

There are also chemical cues that attract the attention of other male wolves. The release of certain pheromones over a period of a day or two signals when the female is ovulating, during which time her mate must be

LEADING THE PACK
Females call the shots, and occasionally the breeding female in a pack will choose not to mate with the dominant male.

especially vigilant. The female will seem disinterested, whereas the male will be stressed and losing sleep, making sure no one else breeds with her. She may breed with another male, but often it's outside the period of peak fertility and so is unlikely to produce pups. There are occasions when a female will mate successfully with two males, resulting in split-paternity litters, although this is rare and hard to document.

Actual mating is called a "tie." The male's penis becomes engorged with blood so he cannot separate from the female for 15–30 minutes, which is an inconveniently long time for cheaters and other interlopers that are keen not to get caught. Premature decoupling can prevent conception, and it's something that must be carefully monitored by researchers during observation. The assumption that the male observed mating with a female must be the father of subsequent offspring isn't necessarily correct.

The pre-breeding season is also a peak period for leaving the pack—after all, if you're not the chosen one, why not leave? Wolf dispersal peaks in fall and

mid-winter as individuals search for better breeding prospects. They strike out on their own to find a wolf of the opposite sex, or to join another pack, where there is a breeding vacancy. Sometimes a wolf comes back not having found greener pastures. This would typically be a male, although females disperse too. On rare occasions, a male will stick with the pack, yet roam surreptitiously away during the breeding season. They visit other packs and try to lure subordinate females away that cannot breed due to low rank within their pack. It's risky; if the lead or resident pack male catches this "cheater," he may try to kill him. Scientists have a hard time measuring how successful these cheating males are. They leave offspring all over the place in different packs and are deadbeat dads, but they might be the most successful of all males. Who said cheating doesn't pay?

A new generation

Gestation lasts 63–65 days. The birthing date can vary because the time period in which the female is able to conceive (the estrus period, usually two weeks) can shift due to mate behavior or availability. If she doesn't breed, she'll pause

AT PLAY

Play is ubiquitous in mammals and serves to develop muscles and improve coordination while also honing social behavior that helps to form dominance hierarchies early on.

and recycle, causing the pups to be born later, all of which contributes to variable birthing, or "whelping." A female will have only two estrus periods each year, and if at the end of the second she isn't pregnant, she'll have to wait until next year—if she is still the breeding female, that is.

Born blind, deaf, toothless, and hairless, pups are helpless (or altricial) and will take all summer to mature. Their eyes open at about two weeks; their small ears are erect at about a month; and they will begin crawling and walking after about three weeks. Their milk teeth emerge after about two weeks and are fully in place by around the third week.

Pups don't crawl from their den until after about three weeks, and in that time they will receive nourishment exclusively from their mother's milk. Once out of their natal den, pups do occasionally nurse from other mothers in the pack—a behavior called communal nursing—although it is rare. Although it isn't unheard of for a pup to be born without the protection of dens, this is rare and risky, and mortality from exposure or even predation is more likely in this situation. Dens are important, but more on that at the end of the chapter.

A collective effort

After the early nursing period, the pups begin to receive regurgitated meat from their mother, father, and other pack members. This type of care, called cooperative breeding, is rare in the animal world and can be crucial to pup survival and development. The extra wolves in the pack, usually offspring from previous years, are referred to as auxiliaries or helpers. They forgo breeding, instead choosing to help raise brothers and sisters, a choice that is called kin selection. It is another way for wolves to spread their genes without breeding. Helpers, like the parents, can bring back a significant portion of food in their stomach: adult wolves are able to carry 22 lbs (10 kg) of ingested meat. This can take pressure off the mother.

The pack members use their stomachs as a kind of shopping bag. It's much easier for a wolf to carry food this way than to transport a leg in its mouth. It also means the food is already chunked up and at times partially digested. It is quite a sight watching a pack member come back from a nighttime hunt:

DINNER TIME
Adult wolves carry food back to the den in their stomach, and pups trigger a regurgitation by licking at the corners of the adult's mouth.

pups rush up licking the side of the mouth of the adult, which triggers a regurgitation, with chunks of meat coming up. The pups scurry around competing with each other to consume the little piles of meat. The adult wolf always looks relieved—not because it dumped that load of meat, but because it is rid of the pups!

When times are tough and food is tight, parents might be forced to choose between the pups and the older offspring. Which do they keep alive: the older offspring, in whose development the parents have invested more; or the pups, who are young and vulnerable, and who need more help in order to survive and are more likely to die? Examples have been documented of both eventualities, and the factors contributing to the parents' decision remain something of a mystery. When times aren't tough, the helpers bring in regurgitated food and

protect the pups from other predators. They also babysit the pups, which serves a couple of functions. As well as providing protection, the helpers play with them, and so support their physical and behavioral development, while also keeping them entertained.

The breeding, or alpha, male plays a significant role in the pack, as the female remains in the den with the pups for the first few weeks of life. Since all offspring in the pack may be his (though this isn't always the case), he is driven to bring back food for all members of the pack. After staying close to the pups for the first few weeks, the mother will start hunting, at which time the weaning period begins.

Weaning starts early because lactation is energetically very expensive (even more so than gestation), and as summer approaches, the condition of the wolf's prey improves, making them less vulnerable to attack and food harder to come by. As a result, the mother wants to wean the pups as soon as possible, without putting them at risk. Given these life-defining trade-offs, the pups are weaned early, at 8–10 weeks (for comparison, cougars are weaned at 12 weeks and bears at 6–8 months), after which they are on an all-meat diet.

Teething pains

I have sat hidden from the wolves, watching them at their den during the period when the pups are maturing and their teeth are emerging. It's painful to watch. You can almost see the mother gritting her teeth as the pups voraciously nurse from her. It must feel like dozens of pins pricking her underside. In fact, I have seen the mother return from a hunt, the pups rush in, and she dutifully nurses without even lying down! She stands, I think, so she can make a quick escape and lie down someplace away from those hungry pups!

From this slow, helpless start, the pups grow fast. There are three growth phases for weight gain, and it varies for females and males. While both sexes grow rapidly at birth, females' growth slows over the next year until maximum weight has been achieved, whereas males continue to gain weight until they are almost five years old, after which time they may lose body mass. A female's weight will remain stable, or she may even gain mass. As the pups transition

FEEDING TIME
Reminiscent of the Roman sculpture of Romulus and Remus, females often feed maturing pups from a standing position, partly out of convenience but also to quickly escape the pups' needle-sharp teeth.

from milk to regurgitated food, they begin hunting on their own around the den or rendezvous site (the place where the adults take the pups after the den). I refer to this site as an above-ground den, as it serves as another place to keep the pups until they mature. It is usually close to water and has cover for concealment and to provide shade. Packs may have one or several of these sites. I have known some packs to have up to four in a summer, although they will typically have only one.

If you were to watch wolves in a rendezvous site, you would see the pups hunting small objects, likely rodents and insects. Adults might even bring in partially alive prey, teaching them early the necessary hunting skills. During their first winter, they will begin participating in hunts in a limited fashion. Although it might look like they are helping, the pups often do little more than cheer the adults on—which is understandable, given that wolves are evolution-

(continued...)

INDEX