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Chapter One

As a Keystone Species

"Keystone: a central stone at the summit of an arch, locking the whole together."
—Oxford English Dictionary

"I learned a fun fact about squirrels. . . . Squirrels cannot find 80 percent of the nuts they hide. Are you kidding me? Is that the greatest thing you've ever heard in your life? First of all, animals aren't supposed to make mistakes. But secondly, I made this realization. . . . Hold your skulls in, because your brains are gonna [f***ing] explode. That's how trees are planted," pronounced comedian Sarah Silverman.

Ernest Thompson Seton, naturalist and pioneering founder of the Boy Scouts of America, wrote in the foreword to his 1922 animal-fiction story *Bannertail: The Story of a Graysquirrel*, "In the nut forests of America, practically every tree was planted by the Graysquirrel, or its kin. No squirrels, no nut-trees." While Seton often anthropomorphized his animals with the human qualities of curiosity, desire, and sympathy, garnering negative and vocal criticism from other naturalists, his observations should not be discounted.

Is Seton or Silverman correct? Perhaps both or neither. Plants rely on seed dispersal for their survival. While some plants have seeds that fly away in the wind, many need a creature, such as a bird or squirrel, to carry away the seed. Whether a seed is picked up on fur and brought inadvertently to a new location, excreted after being eaten, or carried away and planted in the earth, plants have relationships with dispersers. These relationships are crucial to the survival of forest ecosystems; they are crucial to our own survival. Evidence of a seed dispersal crisis in Europe in 2024 indicated that for 30 percent of plant species, most of their dispersers are threatened or declining, demonstrating how vital seed dispersers, such as squirrels, are in our world.

Squirrels are dispersers. They do plant trees, but the process is more complex than both Silverman's and Seton's pronouncements. Squirrels have used their skill at finding food to their advantage, and this demonstrates an "enhanced" cognitive ability. Their food-caching behavior does not lack purpose or direction. And so we must consider the brains of squirrels, how squirrels contribute to the health of our forests, and their role as keystone species.

"Not much goes on in the mind of a squirrel. Huge portions of what is loosely termed 'the squirrel brain' are given over to one thought: food," wrote Kate DiCamillo in *Flora and Ulysses*, a novel centered on a girl and a squirrel that won the John Newbery Medal in 2014. DiCamillo wasn't wrong in describing squirrels' focus and behavior toward food. But that drive for sustenance is present among most animals. From wolves to pelicans, wild creatures constantly think about their next meal. It's a matter of survival. Squirrels aren't an exception. Without that drive for sustenance, they perish. But there is more to the squirrel brain than DiCamillo's description suggests.

Squirrel brain is often used as a derogatory metaphor for someone having scattered and fuzzy thinking without much depth or connection. The truth is much different. Squirrel brains, about the size of a walnut, are substantially more complex. Just as scientists have observed in other creatures, there is a great deal we are uncovering about animal brains and cognition. Squirrel brains are quite large compared with the size of their bodies, quite larger than those of other rodents. This ratio, comparable to that of many primates, demonstrates cognition complexity. This complexity is seen in the way they group their nuts. Squirrels use the method of "spatial chunking," keeping their nuts grouped according to type, to help them remember where they are stashed. Walnuts with walnuts. Hazelnuts with hazelnuts. They also group nuts by size. This is not fuzzy thinking.

Noted US squirrel researcher Michael Steele, along with researchers from Germany and the United Kingdom, explored the "enhanced" cognitive ability of gray squirrels. While they found that some cognitive abilities in gray squirrels, such as solving novel problems, has undergone mild variation as they have adapted to new environments, the previously reported enhanced performance is likely a general characteristic that brings fitness advantages to this species and contributes to their adaptability to new environments. Squirrels demonstrate exceptional problem-solving abilities and have a complex communication system that includes both sound and scent to share information of threats and food sources. "Squirrel brain," then, is far from scattered and fuzzy. And having that brain also has a huge impact on our forests.

In *Bannertail*, Seton captured a squirrel's robust autumn food drive:

"No longer wabbly or vague, as in that first autumn, but fully aroused and dominating was the instinct to gather and bury every precious, separate nut. Bannertail had had to learn slowly and partly by seeing the Redsquirrels making off with the prizes. But he had learned, and his brood had the immediate stimulus of seeing him and their mother at work; and because he was of unusual force, it drove him hard, with an urge that acted like a craze. He worked like mad, seizing, stripping, smelling, appraising, marking, weighing every nut he found."

Anyone, like Seton, who has observed squirrels during autumn can relate to Bannertail's urge that made him act in a "craze" to gather nuts. The urgency squirrels exhibit not only enables them to feed throughout the cold months ahead; their behavior also builds forests.

This wasn't the first time Seton wrote about squirrels. A decade earlier, he included squirrels among sixty mammalian wildlife species in *Life-Histories of Northern Animals: An Account of the Mammals of Manitoba*. Most of his remarks that follow the sections on classification are his personal observations or those of his friends and colleagues. "I am informed by A. K. Fisher that at the southern end at Lake George, in early autumn, it is sometimes an everyday occurrence to see Red-squirrels swimming across the lake, from west to east (about two miles)—never in the opposite direction. The chestnut grows abundantly on the eastern side of the lake, but it is comparatively scarce on the western, and these extensive migrations always take place in years when the yield of chestnuts is large."

Lake George is a thirty-two-mile-long lake in northern New York state's Adirondack Mountains. The mountains make up the southern part of the Eastern Temperate Forests ecoregion, which extends into Maine and eastern Canada and is home to the state's Adirondack Park Forest Preserve. The forests in the park and around Lake George consist of hemlocks, spruces, beeches, pines, and broad-leaved trees. Red squirrels, as well as eastern gray squirrels and two species of flying squirrels, make their home in the forests along with a host of other mammals, including moose, deer, and beavers.

A. K. Fisher's observations of chestnut-searching swimming squirrels in Lake George were not the only observations in the Adirondacks. Early studies of red squirrels in the mountains reported sightings of

squirrels swimming across Big Moose Lake, Long Lake, Brantingham Lake, and Lake George. Seton also included James Higby's observation of June 1877; Higby witnessed as many as fifty squirrels crossing Big Moose Lake.

Another account was documented in Winslow Watson's history of Essex County: "The autumn of 1851 afforded one of these periodical invasions of Essex County. It is well authenticated, that the red-squirrel was constantly seen in the widest parts [about seven miles] of [Lake Champlain], far out from land, swimming towards the shore, as if familiar with the service; their heads above water, and their bushy tails erect and expanded, and apparently spread to the breeze. Reaching land, they stopped for a moment, and relieving their active and vigorous little bodies from the water, by an energetic shake or two, they bounded into the woods, as light and free as if they had made no extraordinary effort."

The massive chestnut trees at the Adirondack lake were appreciated not only by native squirrel species; they also appeared in many works of art at the turn of the century, including Robert Melvin Decker's *Old Chestnuts at Bolton, Lake George*, circa 1890–95. Alfred Stieglitz captured a dying chestnut tree on the eastern edge of Lake George in a 1927 photograph. None of this art captured swimming or climbing squirrels.

However, those chestnut trees, a boon for American red squirrels, were doomed when the nonnative Chinese chestnut tree entered the United States with a lethal fungus.

On an autumn day roughly a century after Stieglitz took that photo, I sat near that site at the southern end of Lake George, reading Diane Ackerman's passages about squirrels in her book *Cultivating Delight*. As with my many other visits to the lake over the years, I did not witness a single red or gray squirrel swimming in the lake. I also haven't seen those majestic chestnuts that propelled the swimming behavior that Seton memorialized in 1909. The lack of chestnut trees altered the composition of the forests and the behavior of the wildlife that depended on them.

Fortunately, those American red squirrels did not completely rely on the chestnuts for their survival. But it is easy to see how we could

have had a different outcome with the population of our common squirrels.

These days, post chestnut tree habitation, red squirrels harvest seeds from Adirondack conifers, including pines, spruces, and firs. They also feed on birch catkins and sugar maple bark and seeds. The Adirondack forests also provide them with nuts from beaked hazelnut and American hazelnut and the berries of northern wild raisin, wintergreen, and partridgeberry. They are regularly seen on all forest trails. The relationship between the American red squirrels and the forests of New York's Adirondack Mountains was also explored in the *Roosevelt Wild Life Annals*. In 1929, field naturalist Robert Hatt wrote about this relationship and our relationship with squirrels in "The Red Squirrel":

> The opinions of people, are, however, anything but unanimous when the status of the squirrel in relation to the community at large is considered. Some see in this impetuous creature only a vivacious forest sprite whose sole claim to existence lies in its charming disregard for all ordinary customs and civilities of life. Others see the squirrel as a destroyer of vast quantities of buds and seeds, a creature barking trees, robbing birds' nests, and driving the more desired gray squirrel from its territory; an animal of little interest as game; a rodent perhaps best dispensed with. Others again note the squirrel burying seeds and nuts for use in the season of scarcity and conclude that, though all unconsciously, it is actually aiding in natural reforestation. Somewhere among these various and conflicting views lies the truth. Like all other wild creatures, the red squirrel has a myriad relations with its environment, some of which are of benefit to a man's community as a whole, some suit the interest of but a few, and others are in themselves wholly undesirable. For this reason the red squirrel is alternately denounced and defended.

In their natural habitat, native squirrel species are a boon for woodlands. That strong relationship can be observed every autumn as they answer the urge to gather food.

While Europe's native Eurasian red squirrels have been front and center in their competition with their North American cousins, the

squirrels there and everywhere have all been working steadily at fulfilling their ecological niche by consuming and dispersing seeds. The two red squirrel cousins are similar in that they are smaller than their gray squirrel relatives. Although they are smaller, the reds are equally important in building forests.

Hatt's missive on the importance of squirrels mirrors the message evoked in the ancient Sanskrit tale the *Ramayana*: No matter how small a creature is, it can make a difference. Squirrels of all species, small and ever present, do much to strengthen the health of our forests.

Solely examining our oak forests demonstrates their importance. A gray squirrel's acorn-caching behavior for food not only benefits the squirrels themselves; since many of those seeds are never consumed by the squirrels, the acorns become the source of new oak trees in the forest. A single oak tree functions as a lifeline to countless other creatures in the forest, including birds, raccoons, snakes, opossums, lizards, moths, butterflies, wasps, and so many more species that depend on leaf litter for shelter and nourishment, demonstrating how squirrels can serve as a keystone species in their forest ecosystem.

By using a scatter hoarding method of burying single nuts in lots of locations, squirrels provide one of the only ways nuts get far enough from the parent tree's shade to have a successful germination. The eventual oak germination leads to the growth of trees with extensive underground root systems that far exceed the width of the tree's canopy. These underground root systems not only stabilize soils but also contribute to carbon sequestration and watershed management. Therefore, squirrels, regardless of species, contribute to forest health in various ways.

While all squirrel species are useful, some are more successful for certain tree species. Take, for instance, New Mexico animal ecologist Jake Goheen's prediction that seven times as many walnuts germinate when scatter hoarding gray squirrels gather them compared with those hoarded by red squirrels. American red squirrels (*Tamiasciurus hudsonicus*) practice larder hoarding, constructing a large storehouse, or midden, of their pine cones and nuts. Their middens don't contribute as greatly to seed dispersal.

Researchers in the Greater Yellowstone Ecosystem discovered that the squirrels also contribute to the health of forests by potentially attracting other seed predators, thereby increasing forest biodiversity as they engineer the ecosystem.

Henry David Thoreau described his observations of squirrels using their caching behavior to plant forests in his essay "The Succession of Forest Trees," found in *Faith in a Seed*:

> On the 24th of September in 1857, as I was paddling down the Assabet in this town, I saw a red squirrel run along the bank under some herbage, with something large in its mouth. It stopped near the foot of a hemlock, within a couple of rods of me, and, hastily pawing a hole with its forefeet, dropped its booty into it, covered it up, and retreated part way up the trunk of the tree. . . . Digging there, I found two green pignuts joined together, with the thick husks on, buried about an inch and a half under the reddish soil of decayed hemlock leaves—just the right depth to plant it. In short, this squirrel was engaged in accomplishing two objects, to wit, laying up a store of winter food for itself and planting a hickory wood for all creation.

The squirrels and chipmunks Thoreau observed while paddling on the Assabet River and at Walden Pond have many descendants, and their caching behavior is still observed today by visitors to the historic site. Many visitors to Thoreau's celebrated pond and woodlands might miss, on their way to swim in his pond, the countless red oaks sprouting up under the trunks of eastern white pines amid clusters of acorn caps, but I was channeling the naturalist on my most recent visit on a hot summer day. The ardent work of the bushy-tailed rodents in the wood was as obvious to me as billboards on a paved highway.

But it isn't just the seemingly indiscriminate acorn planting that increases our carbon capture opportunities. In a 1993 paper titled "Tannins and Partial Consumption of Acorns: Implications for Dispersal of Oaks by Seed Predators," we find that "germination experiments revealed equal or greater germination frequencies for partially consumed acorns than for intact acorns." That's right: Partially intact acorns mean that squirrels took a bite and left the rest behind, and

a tree still sprouted. The authors suggested that "higher tannin levels may render the apical portion less palatable, and thereby increase the probability of embryo survival after attack by seed consumers," also known as squirrels.

In another paper, published in 1986, "Grey Squirrel Food Preferences: The Effects of Tannin and Fat Concentration," biologists Peter D. Smallwood and Wm. David Peters from Ohio State University revealed that free-ranging eastern gray squirrels (*Sciurus carolinensis*) can determine which acorn species are more perishable. This knowledge can lead them to bury an acorn from a red oak, because it will last longer and germinate in the spring, while choosing to eat an acorn from a white oak (*Quercus alba*) because it will germinate earlier in autumn. But scientists, including Smallwood, revisited that finding two years later to investigate whether the size of the acorn made a difference. Was it just a little too large to eat on the spot and perhaps better to stash for later? Eating and caching behavior continues to be one of the more studied squirrel subjects, perhaps because there is so much riding on it, especially at a time when carbon capture is vital to our survival on this planet.

It's been found that many factors besides tannins and fat content go into nut selection. Squirrels consider nut size, nut mass, insect infestation, and food abundance, according to the authors of the landmark 2012 book *Squirrels of the World* by Richard Thorington Jr., John Koprowski, Michael Steele, and James Whatton. To this day, their book serves as the bible of species data for the family Sciuridae of the order Rodentia.

In 2017, in a study conducted at the University of California, Berkeley, scientists Mikel Delgado and Lucia Jacobs turned their attention to eastern fox squirrels (*Sciurus niger*) that buried their food in areas depending on what the food was, sort of like how we sort our own human pantries with baking supplies on one shelf and cans on another. What appears a random act is in fact quite determined, and those squirrel brains aren't as fuzzy as perceived.

Exploring the larder hoarding behavior of American red squirrels led to the discovery that it is intertwined with their social system. They are extremely territorial. These territories are evenly divided among

squirrels, with mother squirrels often bequeathing their territory and middens to their daughters. Unlike the red squirrels, the scatter hoarding grays don't need such a territorial system. But these systems are not universal. Habitat and social structure can change in coniferous forests that are habitat for both reds and grays.

A squirrel above a busy rail trail in New York's Hudson Valley busily nips off oak branch tips filled with acorns as walkers and joggers dodge them below. The squirrel later darts past them on the trail with a nut in its mouth. This scene repeats during autumn as squirrels move about on their quest for food. For observers and researchers, it is yet another puzzling behavior we can add to the list of things we have yet to understand about squirrels.

"I can find no published scientific studies that reveal the reason(s) squirrels cut branch tips," wrote Joe Boggs, an assistant professor at Ohio State University. Boggs doesn't focus on squirrels. Insect pests and landscape problems are his specialty. Boggs addresses the various conjectures about this strange squirrel behavior, including that they "need to gnaw to wear down their ever-growing incisors." But, as he explains, this does not explain the cuts' apparent lack of gnaw marks or the seasonality of the branch nipping in late summer and early fall. Boggs leans toward another explanation. Since most of the nipped twigs include acorns, he surmises that it might be a harvesting technique used to gather the nuts at the smallest branch tips. This is often used by red squirrels to obtain cones.

This gray squirrel behavior plays out throughout the species' range. A forest health specialist with Wisconsin's Department of Natural Resources wrote about reports of oaks losing branch tips in 2018 that revealed tooth marks from squirrels and observations of the rodents clipping and dropping branches.

As often found in less remote deciduous forests, the researchers found that declines in seed dispersers, such as squirrel species, have led to simultaneous reductions in seed dispersal and seedling establishment, emphasizing the crucial role squirrels play in their forest ecosystems.

Studying potential long-term consequences of declining animal mutualists, including squirrels, on the structure and functioning of

Asian tropical forests is crucial for informing conservation strategies to safeguard these vital ecosystems and the species relying on them.

But there is also a need to explore the role of the native red squirrels in the forests of the United Kingdom and northern Italy. As the number of native squirrels decrease as they are replaced by invasive squirrels, how will this affect the health of European forests? So much of what we often discuss focuses on the loss of the iconic native squirrel species and the damage invasive squirrels have caused in native forests. Like reds in North America, Eurasian reds have their own niche. They influence the regeneration of pine woodlands in Europe. The reds are adapted to feed on native pine cones, while the grays feed more on deciduous, broad-leaved trees, such as oaks, in Europe's woodlands.

As with squirrels throughout the world, native species play an essential role in their ecosystems. Many native species of plants have a close ecological and evolutionary relationship with seed-dispersing native squirrels. Tree squirrels are vital seed predators and seed dispersers in both conifer and mixed forests in temperate and boreal biomes. These strong ecological relationships include the eastern fox squirrel (*Sciurus niger*) with longleaf pine (*Pinus palustris*) predation, Abert's squirrel (*Sciurus aberti*) preying on ponderosa pine (*Pinus ponderosa*), and Eurasian red squirrels (*Sciurus vulgaris*) with forest stands of Scotch pine (*Pinus sylvestris*), Corsican pine (*Pinus nigra*) in Belgium, and both Norway spruce (*Picea abies*) and Arolla pine (*Pinus cembra*) in the mixed conifer forests of the Italian Alps.

The Aleppo pine (*Pinus halepensis*) produces large, wingless seeds. The tree relies on nutcrackers and Eurasian red squirrels to disperse the seeds, and the squirrels depend on eating the green immature cones and the cones they scatter hoard for winter and spring. While the squirrels consume lots of seeds, the conifers have been shown to respond by producing nutritious seeds in tough cones that attract these animal partners, ensuring both seed survival and dispersal over wide areas.

These interactions illustrate the complex relationships between squirrels and conifers where squirrels act as both seed predators and seed dispersers, shaping forest dynamics. The protection of these interactions is vital. When connectivity biologist Jeff Gagnon started

working with the Arizona Game and Fish Department to thin the ponderosa pines on Humphreys Peak from a forest fire perspective, he had to consider the squirrels' biology. "We would put little transmitters on the squirrels. I'd go out and track them to see where they were, measure their habitat to conserve those areas and keep them all connected. They are a keystone species in the forest plan," said Gagnon on a ride up to Arizona Snowbowl. The squirrels are prey for the forest's goshawks and seed dispersers for the pines.

But this isn't a story of just reds and grays or woodlands. Squirrels across the world influence their ecosystems.

Researchers traveled to Borneo to study the effects of squirrels and other wildlife on seed dispersal in the Indonesian rainforest, where around thirty squirrel species are found. Similar to the forests in Malaysia, the various squirrel species inhabit the four different layers of the rainforest by day and by night. For example, a selection of species, including the pale giant squirrel (*Ratufa affinis*), inhabit the top canopy layer and are active during the day, while the tufted ground squirrel (*Rheithrosciarus macrotis*) lives on the forest floor and is also active during the day. In contrast, the various flying squirrels each have a layer they inhabit at night, whether it be the canopy, understory, or middle layer.

In the end, hope lies with more conclusive population studies that will allow for greater understanding and possibly better management. Species distribution models (SDMs) are an important mode of population study. A recent study claimed that global Big Data models "are especially important for the many marginalized squirrel species . . . and the high number of endangered and data-deficient species in the world, specifically in tropical regions."

The study asserts that for the global squirrel species, "the habitat needs and ranges are widely unknown [and] not mutually agreed upon. . . . The tropics, particularly the forests of south and southeast Asia, are hotspots of squirrel diversity; however, this region generates the fewest scientific publications on squirrels."

A 2023 study addressed this precisely by including observations of multiple squirrel species, including three-striped ground squirrels, tufted ground squirrels, small-bodied Prevost's squirrels, pale giant squirrels, and red giant flying squirrels on the local forest community.

"I spend a significant amount of time alone, quiet and still, somewhere in a rainforest waiting, watching and writing down what animals are doing at certain fruiting trees," shared the author, Swapna Nelaballi, in an Instagram post in 2020 while in Indonesia's 108,000-hectare (approximately 266,900-acre) Gunung Palung National Park, where sunbears and pangolins live alongside the squirrel species.

Nelaballi and her fellow researcher interviewed local hunters along with observing tufted ground squirrels extracting heavy seeds from the extremely tough *Canarium* fruits "at remarkable speeds and consuming them onsite." Tufted ground squirrels, known locally as Reribu, have powerful jaws. The researchers also observed "three-striped ground squirrels visiting the fruiting *Canarium* tree." They observed that "three-striped ground squirrels were also capable of predation and secondary dispersal of these seeds, although we predominantly recorded caching, theft, and re-caching events by them. This discovery is significant, as it marks a novel finding; prior to our study, apart from few records of bearded pigs and giant squirrels no other mammal, apart from the tufted ground squirrel, had been reported to possess the capability to prey upon *Canarium* seeds. . . .

"Tufted ground squirrels exclusively cached *Canarium* sp. 2 seeds. The composition of the scatter-hoarding community we report mirrors that observed in other Southeast Asian forests." They found that "distant caches were mostly made by three-striped ground squirrels" moving the seeds away from the trees where they fell. "Rodents respond to seed dormancy, and tend to quickly move dormant seeds, take them farther, and re-cache them several times. Our observations support this, as we noted frequent and repeated re-caching of *Canarium* sp. 2 seeds by three-striped ground squirrels."

Their research in the remote rainforest was important in studying "the substantial impact of vertebrate seed predators, particularly large- and small-bodied generalists, on seed mortality and survival dynamics. . . . Lastly, our study suggests that small-bodied squirrels may play a crucial role in providing secondary dispersal services to plants facing limitations in dispersal agents."

While squirrels are beneficial to forest health, they also play a pivotal role in the health of an ecosystem's biodiversity as preferred

prey for many wildlife species. Uinta ground squirrels (*Urocitellus armatus*) alone are a crucial food source for hawks, foxes, coyotes, and sandhill cranes, according to Rhea Cone, director of conservation at Utah's Swaner Preserve and EcoCenter. The ground squirrels, called *chislers* and Potguts, are native to western US meadows, pastures, and shrub-steppe habitats.

It's estimated that prairie dogs, the larger cousins of ground squirrels, contribute to the survival of 150 other species of their predators, such as endangered black-footed ferrets, coyotes, rattlesnakes, and the hawks that flew above the prairie dog colony I visited in Flagstaff, Arizona. "A ferret doesn't eat anything but a prairie dog, and if you don't have prairie dogs, that's really a bad day," said Jessica Simmons, urban wildlife planner for Arizona's Coconino County, on my visit.

Ernest Thompson Seton would have agreed with her. He wrote in *Lives of Game Animals*, "Now that the big Demon of Commerce has declared war on the Prairie-dog, that merry little simpleton of the Plains must go. In a few short years the tiny crater that erupted his annual families will be made no more, the older craters will be abandoned and crumble down to the level of the plain. And with the passing of the Prairie-dog, the Ferret, too, will pass."

While ground squirrels and prairie dogs can be easier prey than fast-moving arboreal squirrels, the nimble climbing squirrels are prey for many avian species, including long-eared owls (*Asio otis*), red-tailed hawks (*Buteo jamaicensis*), peregrine falcons (*Falco peregrinus*), and others in North America, and eagle owls (*Bubo bubo*) and Ural owls (*Strix uralensis*), among others, in Europe. Leopards (*Panthera pardus*), clouded leopards (*Neofelis nebulosa*), and even lion-tailed macaques (*Macaca silenus*) prey on arboreal giant squirrels despite their high perches in India's forests.

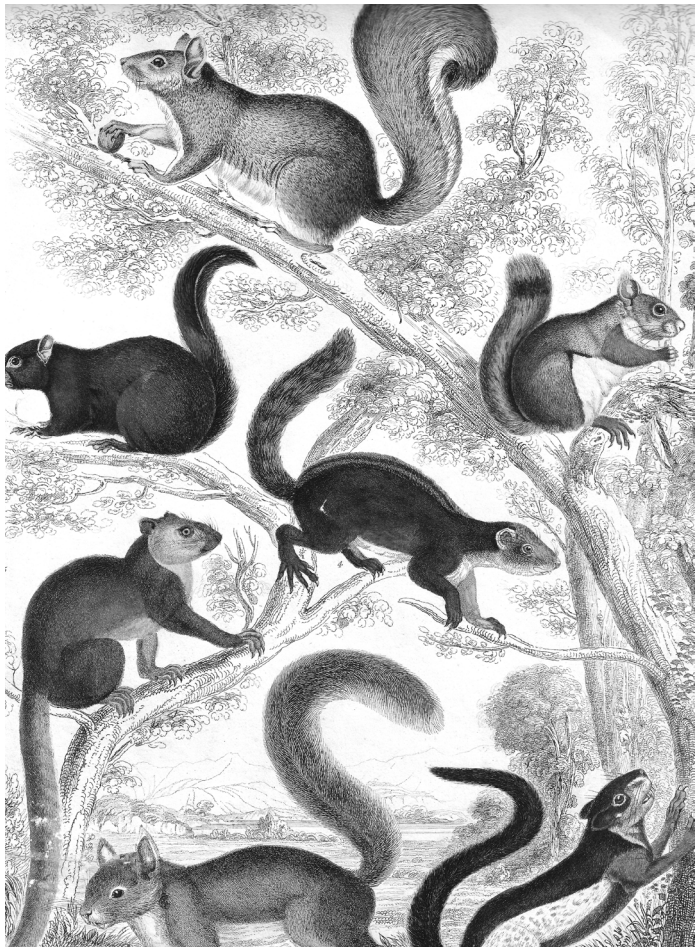
In addition to ground squirrels serving as a food source for many species, the intricate tunnels they dig provide shelter for wildlife, such as burrowing owls, and also aerate the soil, which promotes the health of native plants. Those plants are a crucial protein-rich, digestible vegetation for cattle. But there's the paradox. While ground squirrels, such as the Uinta, perform a strategic role in their ecosystem, those very

holes and tunnels aerating the soil can be a nuisance to humans when they adversely affect landscaping and agriculture.

Our relationship with all squirrels, including arboreal species and ground species, is complex. Humans tend to put their interests first. The question of whether a peaceful coexistence can be obtained with any rodent, but specifically with squirrels, still needs to be determined.

Chapter Two

In the World



"The world is watching."
—Joseph Biden, State of the Union Address, March 7, 2024

One morning years ago, a large stacked pile of long, papery cones mysteriously appeared under our spruce tree. It was as if the entire driveway had been tidied of the scattered cones overnight, like little elves had swept it clean while we slept, creating neat mounds under the trees that had released them. It took us all by surprise. But there weren't elves or human gardeners at work at our house; there were red squirrels.

The small American red squirrel that visited my spruce was one of the three species of tree squirrels classified in the genus *Tamiasciurus*, from the Greek ταμίας, *tamías*, meaning "steward, dispenser," and the Greek for *squirrel*. Scientific names, unlike common names, don't often reflect the species' behavior. *Tamiasciurus hudsonicus*, for example, indicates only where German naturalist Johann Christian Polycarp Erxleben first documented the chattering mammal, in 1771 in North America's Hudson Bay, where it was then placed in the genus among other pine squirrels. John James Audubon referred to it as the Hudson's Bay Squirrel, Chickaree, or Red Squirrel when he portrayed the squirrel in *The Viviparous Quadrupeds of North America [1845–1849]*.

But most call the squirrel by its common names, including chickaree, barking squirrel, pine squirrel, and spruce squirrel, which denote much of the squirrel's vocal behavior. Red squirrels are highly territorial and chatter loudly at anyone or anything passing by their conifer territory. Throughout their lives, American red squirrels (*Tamiasciurus hudsonicus*) perch in pine trees and drop their scraps, the scales and woody bracts of cones, at the base of the tree.

Red squirrels are just one of the squirrel species that live in New York. The others include the common eastern gray squirrel (*Sciurus carolinensis*); two species of elusive, mostly nocturnal flying squirrels, the southern (*Glaucomys volans*) and northern (*Glaucomys sabrinus*) flying squirrels; and other cousins in the squirrel family, the eastern chipmunk (*Tamias striatus*) and the woodchuck (*Marmota monax*), also known as the groundhog or whistle pig. The eastern fox squirrel

(*Sciurus niger*), although primarily a Midwestern species, also has a small population in the western part of the state.

A fungal disease of spruce trees called *Rhizosphaera* needle cast and environmental stress had damaged our New York Hudson Valley spruce trees, forcing us to remove three of them. We resisted the inevitable departure for far too long, hoping in vain that they would recover. Their loss left a gap in our yard and diminished an important source of cones for our red squirrel neighbors.

That pile of cones at the base of my spruce was a carefully gathered midden. These structures, created by squirrels under their favorite tree, can span fifteen to thirty feet in diameter and rise up to four feet tall. Each midden also included the green cones the squirrels had cut from the trees and placed for winter storage. These middens play a role in protecting biodiversity.

My observation of this one common squirrel was just one among millions of observations around the world of hundreds of squirrel species. Those squirrel species are some of the more than 65 living in North America among the 294 squirrel species found naturally worldwide, including such variations of the marvels of evolution as pygmy, dwarf, giant, flying, giant flying, beautiful, sun, groove-toothed, palm, long-nosed, rock, red-checked, American red, tree, striped, and American bush squirrels; chipmunks; ground squirrels; prairie dogs; and the largest, the marmots. In addition, a groundhog famously predicts the beginning of spring, rounding out the full squirrel extended family. It has been said that "the sun never sets on the Sciuridae!"

It can be challenging to keep all these squirrel species and their statuses straight. Most of us are familiar solely with the ones we see regularly, and we assume, mistakenly, that all squirrels are abundant and spend their days scurrying up and down the trunks of trees. That's a partial view, a sliver of our understanding. We must dig into the entire group and its biology to obtain a more accurate view of what constitutes a squirrel.

Squirrels belong to the order Rodentia, and within that order they form the family Sciuridae. As a group, the Sciuridae are diverse and make up 294 species and 51 genera, broken into five subfamilies (Ratufinae, Sciurillinae, Sciurinae, Xerinae, and Callosciurinae). These subfamily

names point to the distinctive characteristics of these squirrels, as with Callosciurinae, the Asiatic squirrels, containing over 60 species named after the genus *Callosciurus*, meaning "beautiful squirrel."

Of all the species in the Sciuridae group, 122 are tree squirrels, and 62 are ground squirrels. With some exceptions, squirrels are characterized as small, bushy-tailed rodents with slender bodies and large eyes, but the variations can be dramatic. Just look at two squirrels from Japan to see this dramatic range: the Japanese pygmy dwarf squirrel (*Pteromys momonga*), weighing less than ten ounces, and the eight-pound Japanese giant flying squirrel (*Petaurista leucogenys*).

Size isn't the single characteristic with such a wide range among squirrel species. Squirrel fur is short and soft but varies in color and thickness among species. Squirrels can be gray, yellow, red, brown, black, or even white, and striped or not striped. Members of the tribe Marmotini—a tribe is a taxonomic rank between subfamily and genus—display a remarkable variety of colors and patterns. Tail length and color also come into play when identifying squirrels. Squirrels of the subfamily Ratufinae, for example, have extra-long tails.

Squirrels' behavior and habitat also contribute to their physical characteristics. Arboreal, or tree, squirrels have long, bushy tails, large ears, and sharp claws for tree climbing. Flying squirrel species are defined by a furred membrane called a patagium that extends between their ankles and wrists and allows them to glide from tree to tree. Ground squirrels have more robust bodies and less bushy tails than tree squirrels. They also have short, sturdy forelimbs to assist them with digging burrows. Whether gray, red, brown, or black, all squirrels have the same skull architecture, including being short with a short front of the skull, called the rostrum, and having an arched profile.

Squirrels are omnivores, eating everything from nuts to plants to meat. While they mainly eat tree seeds and fruit, they'll also eat insects, fungi, buds, shoots, flowers, bark, smaller rodents, bird eggs, caterpillars, snakes, and, much to the dismay of bird-watchers, even small birds.

This ecological role was echoed on a larger scale after Washington state's Mount Saint Helens erupted in 1980, covering over twenty thousand miles with 540 million tons of ash. Three years later, scientists tested whether burrowing rodents could jump-start recovery of the

devastated landscape. They air-dropped endemic pocket gophers—a relative of ground squirrels and prairie dogs—into the area. The gophers' digging behavior was a powerful ecological tool, enhancing soil structure and microbial activity. Six years later, the researchers recorded forty thousand plants flourishing in the spot. In contrast, the surrounding area was still very barren.

Each squirrel species requires a specific habitat for its survival. Gray and fox squirrels, for example, require mid- to late-succession forests for their success. The most productive habitats have a variety of tree species. They will, however, forage in some early successional stages, such as clear-cuts and crop fields. Both species are found on bluffs, riverbanks, and bottomlands. As with many squirrel species, a suitable habitat must contain food sources through all seasons.

Nocturnal flying squirrels have their own habitat needs. Southern flying squirrels often nest in dead beech trees and red oaks. They also make their homes in abandoned bird nests or the dreys (nests) of other squirrels, in woodpecker holes, and in available attics. "You don't encounter them like you would your typical gray squirrel . . . your daytime active squirrels. But they're probably as common if not more common than gray squirrels in some areas," said retired Rhode Island Department of Environmental Management wildlife biologist Charlie Brown about the southern flying squirrels.

Renae Swayser, an environmental educator for Pennsylvania's Wildlands Conservancy, knows this all too well. In February 2024, on a cold Saturday morning, she led a hike to check the squirrel nesting boxes at Thomas Darling Preserve in the Poconos of Pennsylvania, hoping to find endangered northern flying squirrels. The fifty or so nesting boxes had been placed in trees about twenty feet off the ground, and climbing a ladder was necessary to check them. After knocking on them all, she found three southern flying squirrels in one box, but no northern flying squirrels. "Southern flying squirrels are typically the ones that a lot of people [see] if they have cabins in the Poconos, or, you know, a house that they might not visit that often or like a summer house, those are the ones that you find in your attic," she said. While southern flying squirrels might be as common as grays in some areas, northern flying squirrels are endangered. According to the Pennsylvania Game

Commission, an extensive population analysis from 2003 through 2007 found barely thirty-three northern flying squirrels, mainly in the Poconos. Conducting a population study that finds northern flying squirrels, such as the one Swayser is involved with, might move the game commission to develop a plan to help better manage the squirrel's forest habitat.

The white-bellied northern flying squirrel, the other of the two North American flying squirrel species, resides in deciduous and mixed woods from southeastern Canada to Florida. Forest and agricultural tree habitats impact other species of squirrels besides flying squirrels. Woodland habitat management is crucial to preserving our squirrel biodiversity. A similar example is a recent study of threatened Persian squirrels (*Sciurus anomalus*) on the Greek island of Lesvos, which showed that modern olive tree pruning practices jeopardize the squirrel population. The single tree squirrel in the region is the Persian squirrel, with a grayish-brown color on its back, a yellowish-brown color on its belly, and a yellow-brown to deep red tail. It is considered a valuable keystone species on Lesvos, where it lives in centennial olive groves.

All squirrels, including those two flying squirrel species, are active and crucial in their ecosystems. Marmots, prairie dogs, and other ground species dig burrows in shortgrass habitats that become used by many different species. All serve as prey for various predators, from hawks to humans. For example, northern flying squirrels (*Glaucomys sabrinus*) comprise at least 50 percent of the prey in the diets of the critically endangered spotted owl found across forests in the Pacific Northwest states of Oregon and Washington. The loss of this species would significantly impact the population of endangered owls.

Those ground squirrels include species most don't consider to be squirrels. The little chipmunk filling its pouches and appearing in children's *Chip and Dale* cartoons is an example. It is just one of the 25 species of squirrel in the *Tamias* genus, one of the 50 squirrel genera. All chipmunks are squirrels, but not all squirrels are chipmunks. All but one of those 25 species of chipmunks are native to North America. The Siberian chipmunk is the exception and lives in Asia.

Prairie dogs, another ground squirrel species, elicit a wide response from their human neighbors. According to one study, "the prairie dog

has been cussed, discussed, protected, exploited, credited with doing so many good things, and accused of being completely bad." Some call them prairie rats, and others consider them a keystone species. Colonies of prairie dogs, once seen as agricultural pests by the United States government, were poisoned on behalf of agricultural interests. It wasn't until their obligate predator, the black-footed ferrets that once numbered in the tens of thousands, were listed under the Endangered Species Act of 1973 that prairie dog habitat was protected.

Today, prairie dogs are considered a species of greatest conservation need in the four states they inhabit. Drought and plague still hamper prairie dog populations, according to doctoral student Emily Renn. She has worked in Arizona to relocate colonies of Gunnison's prairie dog (*Cynomys gunnisoni*) from urban areas that are threatened by development or destruction to Petrified Forest National Park and other areas with hopes of reestablishing the extirpated wildland colonies. Renn serves as the translocation/coexistence coordinator for Habitat Harmony, an organization that coordinated with the Arizona Game and Fish Department to write the 2015 translocation protocol for Gunnison's prairie dogs in Arizona and authored the 2018 guide to nonlethal management of Gunnison's prairie dogs.

While drought and plague are threats, prairie dogs have other challenges. "They only have one litter of pups, usually three to five pups in spring," Renn told me. "Unlike other rodents that breed regularly, prairie dogs only breed on one day of the whole year. Each individual female is only receptive on one day." If those weren't enough challenges for prairie dog survival, Renn claims that hunter surveys between 2000 and 2006 reported that there were anywhere from 30,000 to 94,000 prairie dogs shot in Arizona each year. Those numbers were acquired through voluntary hunting reporting, so they probably greatly underrepresent what's actually happening, according to Renn. While tribes do shoot prairie dogs for food during the fall, Renn claims that the number has a "small impact compared to target shooting."

Back in my yard, I haven't seen those small reds since we removed the spruce trees. Their absence has left a noticeable void in my daily life. My driveway was messy without them eating and gathering cones for their midden. Pine cones from the remaining trees were strewn

everywhere. Nothing or no one tidied them up. The snowplow pushed them to places they'd never been. More important, my observation showed that our squirrel biodiversity had decreased, a fact that I find deeply troubling.

At most, the survivorship of squirrel juveniles is about 22 percent, meaning that many baby squirrels become prey to other species. Those predators might have gone elsewhere without the squirrels inhabiting my spruce habitat. Red squirrels are avian nest predators on the other side of the predator–prey relationship. When squirrels are in abundance, nestling survivorship may be low. Removing the squirrels from the ecosystem has consequences. I'm not sure what happened to the reds at my home after the spruce trees came down, but I know I do miss them. And I can't stop wondering about the health of the red squirrel population in an area that is losing so many spruce trees beyond the ones at my house. Currently, no studies are exploring the red squirrel population where I live. As with Renn's experience in Arizona, New York relies on hunter records for squirrel population information. Without accurate studies, it is difficult to know the true state of the population, just as I can't measure the state of red squirrels by what is happening at my house. This underscores the urgent need for scientific studies to provide a more complete picture.

Squirrels, though common, play a crucial role in our ecosystem. We often don't notice their presence until they are gone. And mine were gone. I didn't notice their disappearance until the cones from my remaining spruce trees flooded my driveway. Although they have lived beside us forever, squirrels are rarely considered beyond National Squirrel Appreciation Day or studies by wildlife biologists.

Biologist Thaddeus McRae's comment that squirrels are background rings true. Are squirrels now just white noise in the swelling soundtrack of our noisy lives? As headlines scream of wildfires, floods, and a planet unraveling under the weight of human-induced climate collapse, who still pauses to wonder about the fate of squirrels? It seems entirely possible that these familiar creatures—and many others—are vanishing quietly, drowned out by the louder crises we face and the accelerating loss of life around us.

Given the remarkably minimal scientific interest in them, it's clear

that we need to focus more scientific scrutiny on squirrels before we lose species most stressed by humans and climate change. Worldwide, squirrel species might be the most mysterious creatures we see every day. In this era of worldwide biodiversity loss, it's imperative to bring squirrels out of the background and into our attention, and take action to protect them.

Imagine an annual accounting, like the State of the State, each year. A similar event for our global squirrels would present a clear view of how our squirrels are faring, including which ones are struggling and which are thriving.

A similar event, the International Colloquium on Arboreal Squirrels, does exist, but unfortunately, it doesn't include all squirrel species and doesn't occur annually. The last one was held before the COVID-19 pandemic, interrupting the schedule of having it every three years. Without it, we're lacking vital information.

"From deer stands, I have often watched squirrels rustle about in the leaves beneath me, or heard them in the trees above and behind me as they scold me as an intruder, so I believe that our countryside has no squirrel deficiency," wrote Steve Gilliland from Kansas in 2024. Is Gilliland right—if we see squirrels around us, should we assume there is an abundance? Or should we believe there isn't if we don't, as in my case?

This thinking pattern corresponds to the way many people think about climate change. If it is cold at my house, does it mean that Earth isn't warming? Remember when Senator James Inhofe from Oklahoma brought a snowball into the US Senate in 2015 to demonstrate that the globe is not warming? "I asked the chair, do you know what this is? It's a snowball just from outside here. So it's very, very cold out. Very unseasonable." Are our casual squirrel observations just as tone-deaf?

I recognized that the lack of red squirrels at my house didn't indicate a decrease in the population locally or regionally. I'd have to search for information from the experts, the state agency tasked with conservation, to test my hypothesis that the struggling and dying spruce trees in my area might adversely affect the local red squirrel population.

If my hypothesis was correct, would the local annual squirrel hunt

be allowed to continue? Indeed, if the population dipped, I believed that it would certainly be curtailed.

However, the experts at the New York State Department of Environmental Conservation did not have the answers I needed. As mentioned, I learned that the department, as in Arizona, did not study the population; the agency relied solely on hunters for the status of the state's squirrel populations. It had nothing unusual to report or any completed scientific studies.

In addition, the local squirrel hunt, the Squirrel Scramble, was indeed proceeding. It advertised that hunters would receive extra points for killing red or black squirrels. Black squirrels are a melanistic subgroup of squirrels with black fur, not a separate squirrel species. They are a rarer color variation of the eastern gray squirrel.

At that time, I didn't know that the local squirrel-hunting contest would be the last one in New York state. It wasn't ending because of concern about the squirrel population. Instead, after continued pleas from animal protection and conservation organizations and legislation passed by the state legislature, New York's governor, Kathy Hochul, signed legislation S.4099/A.2917 on December 22, 2023, to protect the state's wildlife by making hunting contests, competitions, tournaments, and derbies that allowed for the taking of large numbers of wildlife unlawful.

In a press release, Governor Hochul said, "Protecting wildlife is critical to fostering the integrity and resilience of our environment and outdoor recreation economy. This legislation establishes strong safeguards for our state's precious wildlife species and protects our important fishing and hunting traditions." Humane World for Animals estimates that at least 57,000 animals, many of them, like squirrels, considered a "nuisance," are killed yearly in wildlife killing contests and competitions. With more states eliminating hunting contests, that total number is down from more than 60,000.

Although the legislation in New York excludes contests for hunting white-tailed deer, turkeys, and bears and for fishing contests, it will affect the populations of other species, including squirrels. "Today is a win for every animal that was previously targeted by these cruel contests," said Regan Downey, director of education at the Wolf Conservation

Center. "We applaud Gov. Hochul's decision to sign A.2917/S.4099 into law. New Yorkers value humane and science-based approaches to wildlife management, and we are thankful to finally have a policy that reflects these values in our backyard. Killing contests have no place in the 21st century, nor do they have a place in New York."

The new law makes it illegal "for an individual to organize, sponsor, conduct, promote or participate in any contest, competition, tournament or derby with the objective of taking or hunting wildlife for prizes, inducement or entertainment. Any wildlife killed during these activities become the property of the New York State Department of Environmental Conservation."

Amid backlash from those who feel these hunts are a popular and family-friendly way of introducing their children to hunting, New York state became the tenth state to stop the slaughter of wildlife for cash and prizes, following a recent Oregon ban of contests on state land. California was the first state in the country to ban wildlife contests, in 2014. Illinois and New Jersey were following New York's lead in 2024 to ban hunting contests through legislation rather than state agency rules. New Jersey state representative Anna Moeller, the sponsor of the New Jersey bill, said to a reporter from the *New Hampshire Bulletin*, "We support hunting that's done in a sustainable and responsible way. When you're wiping out large numbers of animals at a time, you're creating an imbalance, and oftentimes we find there's harmful consequences from being so reckless."

In March 2024, New Jersey introduced N.J. Admin. Code § 7:25-5.22, stating, "No person shall have in possession, kill, attempt to take, hunt for, pursue, shoot, shoot at, trap, or attempt to trap any wild mammal or wild birds unless an open season for the taking of such birds or mammals has been declared by the New Jersey Fish and Game Laws or Code and then only during the respective open seasons." The introduced legislation can be viewed as an animal bill of rights. It prohibits any person from organizing, sponsoring, promoting, conducting, or participating in a competitive event at which participants harass or take covered wildlife, except in conjunction with an authorized field day event.

On January 23, 2024, a public radio program focused on a popular

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