Choices

My neighbor, Paulie and I communicate mostly by shouting. I'll be outside unpacking the car and she'll stick her head out of the barn and yell across the road, "How was your trip? Big rain while you were gone, the squash in the garden are going crazy—help yourself." Her head pops back into the barn before I can answer. She takes a dim view of my gallivanting around, but keeps a good eye on the place while I'm gone. While I'm out stacking firewood or planting beans, I'll catch sight of her blaze orange cap and call across the road to her with news of a downed fenceline I discovered up by the pond. Our shouts carry the shorthand affection we have for each other. Over the years it's been a telegraph from my side of the road to hers, carrying messages of kids growing up, parents growing old, breakdowns of the manure spreader, and news of the killdeer nesting in the pasture. On 9/11 I ran from my TV to the barn where we hugged and cried for a short moment until the feed truck arrived and brought us back to the immediate need of calves to be fed.

My old house and her old barn, in the little town of Fabius, New York, were once part of the same farm, starting way back in 1823. They share the shade of the same big maples and are watered by a common spring. We've brought them back from the brink of decay together, so it's fitting that we, too, are friends. Sometimes, when the weather is nice, we stand with arms folded in the middle of the road to talk, shooing barn cats out of the road and holding up traffic, which consists of the occasional haywagon or the milk truck. Our dirty work gloves are pulled off as we soak up the sun and the talk and are pulled back on again as we turn away. On the rare occasions when we do talk on the phone she forgets she's not hollering from the barn and I have to hold the phone a foot from my ear.

As observant neighbors we know a lot about each other. She just shakes her head and laughs over my field seasons spent earnestly investigating the reproductive choices of mosses. All the while she and her husband Ed are milking 86 head, raising corn, shearing sheep, and building a heifer barn. Just this morning, we met down at my mailbox and had a moment to talk while she was waiting for the AI man. "Artificial Intelligence?" I asked with a raised eyebrow. This cracked her up, one more sign of the detached ignorance of her neighbor, the professor. The white panel truck splashed over the potholes to the barn, a picture of a bull on the side. "Artificial Insemination," she shouted over her shoulder as we walked back into our worlds on opposite sides of the road. "Your mosses may have reproductive choices, but my cows sure don't."

Mosses do exhibit the entire range of reproductive behaviors from uninhibited sexual frenzy to puritanical abstention. There are sexually active species churning out millions of offspring at a time and celibate species in which sexual reproduction has never been observed. Transexuality is not unheard of; some species alter their gender quite freely.

Plant ecologists measure a plant's enthusiasm for sexual reproduction with an index known as reproductive effort. This measure is simply the proportion of the plant's total body weight which is dedicated to sexual reproduction. For example, our maple tree allocates much more of its energy to production of wood than to its tiny flowers and helicopter seeds that twirl to the ground on the breeze. In contrast, the dandelion in the pasture has a very high reproductive effort, with much of the plant's mass tied up in yellow flowers, followed by drifts of fluffy seeds.

The energy allocated to reproduction can be spent in a variety of ways. The same number of calories could be used to make a few large offspring that the parents invest in heavily. Alternatively, some are more profligate, spending their energy on a large number of tiny, poorly provisioned offspring. Paulie has strong opinions on those who have children that they don't adequately support. One of the barn cats, a long-haired beauty named Blue, seems to take the attitude that kittens are a disposable commodity. She has litter after litter, but can't be bothered to nurse them and leaves them to fend for themselves. Mosses like *Ceratodon* take the same approach. On a patch of disturbed ground along the cow track to the barn, the leaves of *Ceratodon purpureus* are barely visible under the dense swath of sporophytes it produces all year long. But each spore is so small and poorly provisioned that, like Blue's kittens, it has a vanishingly small chance of surviving. Fortunately, there is among the barn cats a paragon of good mothering, Oscar. She's the old lady of the haymow, and carefully tends her single litter, and willingly adopts Blue's orphans as her own. For this, Oscar earns a place at the milk dish at milking time.

Paulie would approve of a moss like *Anomodon*, growing on the shaded rock wall behind the barn. This species delays its spore production until later in life, preferring to allocate its resources to growth and survival, rather than unfettered reproduction.

The two strategies of high and low reproductive effort are usually associated with a particular environment. In an unstable, disturbed habitat, evolution will tend to favor those species that produce many small highly dispersable offspring. The unpredictable nature of the habitat, like the *Ceratodon* near a cow path, means that the adults have a high risk of dying by disturbance, and so it is advantageous to reproduce quickly and send your progeny off to greener pastures. The destination of those wind-blown spores is unknown, but is likely quite different from the path edge of the parents. Sexual reproduction also conveys a strong advantage by mixing up the parents' genes into new combinations. Every spore is like a lottery ticket. Some will be good combinations, some will be bad, but the gamble pays off with millions of offspring spread randomly over the landscape. One will surely find a patch of ground where its novel genetic formula will bring it success. Sexual reproduction creates variety, a distinct advantage in an unpredictable world. However, sexual reproduction also incurs some costs. In creation of egg and sperm, only half of the parents' successful genes are passed to the offspring, and those genes are shuffled in the lottery of sexual reproduction.

In her muddy boots and manure-spattered jacket, Paulie doesn't fit the white-coat image of genetic engineering, and yet she is working at the forefront of its application. A Cornell grad, she has bred an award-winning herd of Holsteins with impeccable genetic pedigrees. Rather than lose this hard-won genetic advantage by mating her best cows with any old bull, she is using artificial insemination and then transferring the identical embryos to surrogate mothers in the herd. In this way, she will develop a herd with little variability, perpetuating the successful genotypes that would have been scrambled by ordinary sexual reproduction. Such cloning is a recent development in dairy production, but mosses have been doing it since the Devonian era.

Reproductive strategies that limit variation and preserve the parents' favorable gene combinations are commonplace among the mosses. The rock wall behind the barn has been undisturbed since the first farm owners built it 179 years ago. In such a steady, predictable habitat a steady, predictable way of life is most successful. The *Anomodon* mat that lives there has had nearly two centuries to prove that it bears a genetic makeup well suited to that particular spot. Energy devoted to frequent sexual reproduction would essentially be wasted here, by producing wind-blown spores of potentially unfit genotypes, which would simply be lost on the wind. In a stable, favorable environment, it is better to invest that energy in growth and clonal expansion of the existing long-lived moss, preserving the tried and true genotype, like pedigreed cows.

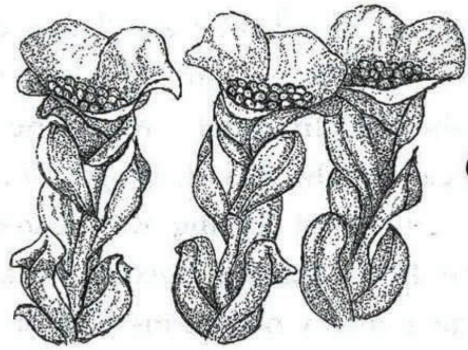
Natural selection is constantly acting upon the pool of individuals that make up a population, and only the most fit survive. Burying generations of barn cats who never learned to cross the road, or stillborn calves, clearly reveals the hand of natural selection. On such occasions, Paulie brushes off the loss with a practiced line. "If you're going to have livestock, you're going to have deadstock." Despite her bluster, Paulie's menagerie tells a different story. Not all of her animals are the cream of the crop. One stall is home for an old cow, blind now for many years. Her name is Helen. She's a good old girl and with the time-honored nose-to-tail guidance system she stills goes out to pasture with the others. And then there's Cornellie, the orphaned lamb whom Paulie brought home in diapers to sleep by the woodstove until it was big enough to survive. But, in nature, there is rarely a Paulie who spares the unfit from the scythe of natural selection. So I've been looking at the reproductive choices made by mosses in light of natural selection. Which choices result in survival and which are steps toward extinction?

Chance and our choices have brought Paulie and I together, converging for some reason on this old hill farm. Something about the way the house nestles in the hill sheltered from the wind, or the way the morning sun pours over the meadow. She fled the expectations of Boston family and chose the intense flavor of farming over a career as an animal physiologist. I flew here like a homing pigeon after a sad divorce with the fervor to start again, on my own terms. Our dreams have found a home here. Paulie recreates her self-sufficiency every single day and revels in the company of animals. And here my microscopes can share the table with blackberry pies.

Up in the hemlock swamp at the top of our pasture, the woods are fenced from grazing. Paulie is mowing hay in the adjacent field, the tractor rumbling along. I wave to her as I duck under the barbed wire and into the woods. A few steps into the trees and a hush descends with the green filtered light. The hemlock timbers which built my house and Paulie's barn were cut here generations ago. The old logs and decaying stumps are covered with one of my very favorite mosses, *Tetraphis pellucida*. I know of no moss more charged with well-being than *Tetraphis*. Its young leaves are luminous as dewdrops and swollen with water. The species epithet "*pellucida*" reflects this watery quality of transparency. Its sturdy little shoots are clean and simple and stand upright in a hopeful sort of way. Each stem is no more than a centimeter tall with a dozen or so spoon-shaped leaves arranged like an open spiral staircase ascending the stem.

In contrast to most mosses, which have adopted a particular lifestyle and stuck with it, *Tetraphis* is remarkable for its flexibility in making reproductive choices, sexual and otherwise. *Tetraphis* is unique in having specialized means of both sexual and asexual reproduction, standing in the middle of the road of reproductive options.

Most mosses have the ability to clone themselves from broken-off leaves or other torn fragments. These bits of debris can grow into new adults that are genetically identical to the parents, an advantage in a constant environment. The clones remain near the parents and have little ability to venture into new territory. Cloning by dismemberment may be effective but it is a decidedly crude and random way to send genes into the future. *Tetraphis* however, is the aristocrat of asexual



Gemmae cups of Tetraphis pellucida

reproduction, possessed of a beautifully sculpted design for cloning itself. When I kneel to look closely at the patches of *Tetraphis* on the old stumps, I see that the surface of the colonies is sprinkled with what look like tiny green cups. These gemmae cups, formed at the ends of the upright shoots, resemble miniature bird's nests, complete with a clutch of tiny emerald eggs. The nest or gemmae cup is a circular bowl made of overlapping leaves and nestled within it lie the egg-like gemmae. Each gemma is a roundish mass of only ten to twelve cells, which catch the light and shimmer. Already moist and photosynthesizing, each gemma is poised to establish itself as a new plant, cloned from its parent. It rests in the nest, waiting. Waiting for an event that will propel it away from its parent, where there's room to grow and start its own family.

When the skies darken and the thunder rolls, the time is at hand. Great big raindrops pelt the forest floor, and ants and gnats dive into mosses for shelter, lest they be squashed by the momentum of the raindrops. But sturdy little *Tetraphis* waits expectantly, for it is designed to harness the power of a raindrop. When a gemmae cup receives a direct hit, the raindrop breaks loose the gemmae and propels them outward, leaving the nest empty. The gemmae can be splashed up to fifteen centimeters away, which isn't bad for a plant only one centimeter tall. In a favorable location, the gemmae can regenerate an entire new plant in the span of a single summer. In comparison to spores, which are at the mercy of a fickle breeze that deposits them anywhere, a rock or a rooftop or the middle of a lake, gemmae are more likely to land in the same neighborhood as their parents. As clonal propagules, the gemmae carry a combination of genes that has already proven successful on this stump.

Sexual shoots of Tetraphis pellucida bearing sporophytes

In contrast, the spores produced by the sexual mixing of the parents' genes are a myriad of genetic combinations, a powder of potential sent off to seek its fortune in the unknown realm beyond the stump. There are other patches of *Tetraphis* on the very same stump which are the cinnamon color of old redwood. They take their rusty tint from the dense swath of sporophytes which rise from the green shoots below. Each sporophyte ends in a capsule shaped like an open jar. The mouth of the jar is ringed with four rusty teeth, from which the name *Tetraphis* ("four teeth") is taken. When the capsule is ripe, millions of spores will be released onto the breeze. The product of sex, the spores will carry the shuffled genes far from their parents. While these spores have the advantage of variety and distance, their success rate is exceedingly small. The tiny spores, even when carefully sown on a suitable site like another hemlock stump, yield only one plant for every 800,000 spores sown. There is clearly a tradeoff between size and success. The gemmae are hundreds of times larger than spores, and hundreds of times more effective in generating new plants. The large size and active metabolism of the gemmae, in comparison to spores, give them a higher chance of success. In experiments, I've found that one in ten gemmae survive to establish a new plant.

I can hear that the sound of the hayrake has stopped and Paulie comes down the sun-dappled path to see what I'm up to, grateful for a respite from the summer sun. I hand her my water bottle and she drinks deeply, wiping her mouth on the back of her hand and bending down to sit on a hemlock stump. I show her the two kinds of *Tetraphis*, the asexual colonies with reliable "stay at home" gemmae and the highly sexual colonies, sending their adventurous offspring off on the breeze.

She just nods her head and laughs. It's a story she knows very well. Her daughter, so very like her mother, has decided to stay on and work the land alongside her parents after college. Her oldest son, however, has flown the nest to become a teacher at the other end of the state, having no interest at all in days that start with milking before sunrise and end long after the cows come home.

When I look at logs and stumps covered with *Tetraphis*, there is a striking pattern. The two forms, gemmae and spores, occur in distinct patches, almost never intermingling. Since each reproductive strategy, clonal and sexual, is usually associated with a very different environment and with individual species, I wonder at the cause of this pattern. Why should the same species adopt a clonal lifestyle in one patch and a sexual lifestyle in another on the very same stump? Why does natural selection allow two opposite behaviors to coexist in the same plant? This question led me into a long and intimate relationship with *Tetraphis*, one of fascination and of respect where *Tetraphis* taught me a great deal about doing science.

I suspected right away that the cause of the reproductive patchiness was some aspect of the physical environment. Perhaps differences in moisture or nutrients in the decaying wood caused different forms of reproduction. So I laboriously measured environmental factors to see which one was correlated with either sexual or clonal behavior. I lugged around a pH meter, a light meter, a pyschrometer, and bagged samples of decaying log to take back to the lab for an analysis of moisture and nutrients. Months of expectant data analysis later, I discovered that there was no correlation whatsoever. There seemed to be no rhyme nor reason to *Tetraphis'* reproductive choice. But if there's anything that I've learned from the woods, it's that there is no pattern without a meaning. To find it, I needed to try and see like a moss and not like a human.

In traditional indigenous communities, learning takes a form very different from that in the American public education system. Children learn by watching, by listening, and by experience. They are expected to learn from all members of the community, human and non. To ask a direct question is often considered rude. Knowledge cannot be taken; it must instead be given. Knowledge is bestowed by a teacher only when the student is ready to receive it. Much learning takes place by patient observation, discerning pattern and its meaning by experience. It is understood that there are many versions of truth, and that each reality may be true for each teller. It's important to understand the perspective of each source of knowledge. The scientific method I was taught in school is like asking a direct question, disrespectfully demanding knowledge rather than waiting for it to be revealed. From *Tetraphis*, I began to understand how to learn differently, to let the mosses tell their story, rather than wring it from them.

Mosses don't speak our language, they don't experience the world the way we do. So in order to learn from them I chose to adopt a different pace, an experiment that would take years, not months. To me, a good experiment is like a good conversation. Each listener creates an opening for the other's story to be told. So, to learn about how *Tetraphis* makes reproductive choices, I tried to listen to its story. I had understood *Tetraphis* colonies from the human perspective, as clumps in various stages of reproduction. And I had learned little by doing so. Rather than looking at the clump as an entity, I had to recognize that the clump was simply an arbitrary unit that was convenient for me, but had little meaning for the moss. Mosses experience the world as individual stems and to understand their lives I needed to make my observations at the same scale.

So I began the laborious work of inventorying the individual shoots in hundreds and hundreds of *Tetraphis* colonies. I took pains to see every patch of *Tetraphis* I sampled as a family of individuals. Every single stem was counted, and every shoot was categorized by its gender, its stage of development, and its mode of reproduction, gemmae or spores. I wonder how many shoots I've counted in all—probably millions. A dense colony of *Tetraphis* can have three hundred shoots per square centimeter. And then each colony was marked. I found that the plastic cocktail swords which impale olives in martinis make the best markers. They won't decay and the bright pink plastic makes them easy to locate the next year. And besides, I like to imagine the conversations of hikers who encounter mossy logs decorated with swizzle sticks.

The next year, I went back and found each of the marked colonies and counted them again. In notebook after notebook, I recorded the changes in their lives. And then again the year after that. Slowly, with my knees in the duff and my nose on the stump, I was starting to think like a moss.

I think that Paulie would be the first to understand this. Making a living as a dairy farmer on a few hilly acres is a tough proposition. She has been successful because she knows her herd, not as a clump, but as individuals. There's not a numbered ear tag on the farm; she knows every cow by name. She can spot when Madge is ready to calve, just by the way she walks down the hill. The time spent to know their habits and their needs gives her a competitive edge over the industrial-scale dairy farmers.

My notebooks record the fate of each patch, a changing census of the tiny moss community. With patient watching, and no direct questions, year by year, *Tetraphis* began to tell its own story. Colonies on bare wood start out with sparse and widely scattered shoots, a community with plenty of elbow room. In these low-density patches of fifty individuals in a square-centimeter sample, virtually every shoot bears a gemmae cup at its tip. The falling gemmae grow into more thrifty young shoots and by the time I return the next year the stems have gotten crowded. In colony after colony, I notice a remarkable pattern. With crowding, the gemmae disappear. There is an abrupt switch from making gemmae to making female shoots. Crowding seems to trigger the onset of sexual reproduction. With a populous colony of females and scattered males, it's not long before sporophytes appear. The colony has transformed itself from the vibrant green of gemmiferous shoots to the rusty color of spore production. When I return the next year, the colony has become even more crowded, approaching three hundred stems per square centimeter. This high density seems to trigger a radical shift in sexual expression. Now, the only shoots produced are male, with not a female or a gemmiferous shoot in sight. We discovered that *Tetraphis* is a sequential hermaphrodite, changing its gender from female to male as the colony gets crowded. This switching of gender with population density had been observed in certain fish, but never before in mosses.

In trying to piece together *Tetraphis*' story, I wanted to be sure that I understood what was going on, that the choice of having sex or making gemmae was really determined by the density of the colony. If that were true, then if I could change the density, the mosses should change behavior. Perhaps I could ask an indirect question, and perhaps they would answer. To ask the question in the language of mosses, I took a cue from Paulie's woods.

A few years ago, when she needed cash for the new heifer barn, she decided to harvest some trees from her woodlot. She shopped around carefully for a logger committed to low-impact harvest, someone who would take good care of the woods. They cut timber in winter, scattering their openings, and made a clean job of it. In the springs that followed, the thinned woods had a carpet of snowy white Trillium and yellow trout lilies blooming under the leafy canopy. The lowered density had let in more light and rejuvenated the old stand.

Like a logger in miniature, I sat poised with fine forceps over the old, dense *Tetraphis* patches. One by one, I plucked out single shoots of *Tetraphis*, stem by stem, until the density was reduced by half. And then I let them be, returning the next year to observe if they had given me an answer to my question. The unthinned patches of *Tetraphis* remained male and had started to turn brown. But the patches where I'd opened the moss canopy by thinning were green and vibrant. The holes I'd made in the *Tetraphis* turf were being filled with thrifty young shoots, bearing gemmae cups at their tips. The mosses had answered, in their own way. Low density is a time for gemmae, high density for spores.

The transformation to being male appears to have adverse consequences. Over and over, I observed that the dense male patches were starting to die back, becoming dry and brown. These tired male colonies, spent with reproduction, were then easily invaded by other mosses on the log. Sometimes, I'd find the telltale swizzle sticks in a patch where old male colonies of *Tetraphis* had disappeared, obliterated by the advance of carpet mosses. Why would *Tetraphis* adopt a sexual lifestyle that seemed to doom it ultimately to fail, headed for local extinction?

On many occasions, I'd return to a familiar stump only to find that the carefully marked patch of *Tetraphis* had vanished. In its place was a clean, bare surface of newly exposed wood. Scrambling around on my knees, I found the patch of *Tetraphis*, still impaled by its cocktail sword, at the base of the stump, where it had tumbled in a small avalanche of decayed wood. These stumps and logs were a landscape in motion. The process of decay and the activity of animals were constantly causing the logs to fall away, piece by piece. The stumps looked like small mountains, forested by mosses, with a talus slope of decayed chunks lying like fallen boulders at their base. Blocks of old wood fell away, carrying their surface cover of *Tetraphis* and creating the bare places I'd noticed. And what became of such open spaces, these patches of new wood? Looking closely, I could see that they were sprinkled with gemmae, little green eggs that had splashed into the gaps in the old *Tetraphis* cover. In the aftermath of disturbance, the seeds were sown for the next wave of *Tetraphis*.

When I stop by the barn to buy a carton of fresh brown eggs, Paulie is just coming back from a meeting. We stand there in the sun, admiring the morning glories climbing up the side of the old silo. She heard some talk of opening a casino over in the next county and we laugh about the unwary throwing their money away on chance. "Heck," she says, "we don't have to go to the casino to gamble. Farming is like blackjack, year in and year out." Milk prices are notoriously unreliable, and feed costs can triple from one year to the next. Farm income can fluctuate like clouds passing over the sun, but college tuition only goes up. That's where the Christmas trees come in, and the sheep and the feed corn. To buffer against uncertainty, Ed and Paulie run a diversified farm. The cows are the mainstay but in years when milk prices are down, maybe the lamb market will pay the kids' tuition, or maybe the Christmas trees. They survive in an era of disappearing family farms by a resilience rooted in flexibility, where stability comes from diversity.

It's the same for *Tetraphis*, a moss that is hedging its bets in an unpredictable landscape where a landslide of decay can disrupt years of steady growth. It achieves stability in an unstable habitat by freely switching between reproductive strategies. When the colony is sparse and there is lots of open space, it pays to be clonal. The gemmae can occupy the bare wood more quickly than any spore and maintain a competitive advantage against other moss species. But when it gets crowded, the only offspring that have a chance are spores. And so sexual reproduction is begun, to produce spores of divergent genetic makeup that will be blown away from the parents in their dwindling habitat. It's a gamble that any spore will land on a suitable log and be able to start a new colony. But it's a sure thing that without disturbance the colony will become extinct if it stays in one place.

The other mosses of less imaginative reproduction are slowly creeping closer, ready to engulf little *Tetraphis*. But *Tetraphis* has chosen its habitat well, taking full advantage of the rot which reliably causes disturbances to the log. Just about the time that the spent colony of *Tetraphis* is about to succumb to competitors, the face of the log peels away in a landslide of decay, exposing fresh new wood as it eliminates a patch of competitors and *Tetraphis* as well. If *Tetraphis* had to rely on spores to colonize these open spaces, its competitors would more often win the race for space. But just a few centimeters away stands a patch of *Tetraphis* in its clonal phase. With the next rain, gemmae are splashed into the opening and rapidly produce a new patch of vibrant green shoots. Decay renews the open space, and in accord, *Tetraphis* renews itself. *Tetraphis* plays both sides of the game, producing gemmae for short-term profit and spores for long-term advantage. In this changeable habitat, natural selection favors flexibility rather than commitment to a single reproductive choice. Paradoxically, those species adapted to a specialized lifestyle come and go, but *Tetraphis* persists by keeping its options open and maintaining its freedom of choice.

Maybe it's the same with our old farm, persisting now for almost two centuries. Generations of other women before us have shooed barn cats out of the road, planted lilacs, and raised their children under these maples. The old bull has been replaced by the AI man, and the cistern by a well. But the world is still unpredictable and still we survive by the grace of chance and the strength of our choices.