Dancing in the Dome

Males are lured by food and sex into erotic contests and deadly brawls

by Paul J. Watson

The best time to see the webs of the Sierra dome spider at my Montana study site is just after a summer dawn, when the sun's rays stream at a low angle through the undergrowth. Within a 150-foot radius of my cabin at the Flathead Lake Biological Station, perhaps 300 female spiders spin their glistening dome webs between low, leafless branches. Webs are usually four to sixteen inches wide, with a characteristic dome structure one to three inches tall near their centers. Each day, the spiders clean, renovate, and enlarge their webs, giving meticulous care to the dome. The undersurface is their living space, where they annually reenact a silent, ancient drama of sex and combat.

My study site is on a small, forested peninsula that juts into an enormous glacial lake. The cool, shoreline location harbors a dense spider population, as well as swarms of insect prey, such as mayflies, caddis flies, gnats, midges and mosquitoes, that begin life in the lake and its many inflowing streams. For more than a decade I have come to this forest of ponderosa pine and Douglas fir, with its understory of honeysuckle, rose, and ninebark, to study the Sierra dome spider's intricate reproductive life.

At first glance, the female appears to lead an easy existence nestled within the relative security of her silken labyrinth, quietly waiting for prey and for wandering males to find and court her. But although she is visited by ten to twenty eager suitors over the course of the summer, she typically mates with only three or four. And of these, often only one male will sire the majority of her brood. Other males may share in fathering perhaps 20 to 30 percent of her offspring or none at all.

I wondered why females typically mate with several males, and how they select which will sire their offspring.

In September and October, the female spider produces a silken egg case, in which she lays 20 to 100 eggs, depending on how successful a forager she has been. Afterward, she binds the whole mass in silk. When the eggs hatch thirteen days later, the spiderlings, known as first instars, stay within the egg case. They soon molt to a second stage, but still remain in the silken case throughout the winter. When they finally emerge in March, juveniles of both sexes live solitarily for a time and seek out sites for their own domed webs. After growing through five or six additional molts, the spiders reach sexual maturity in late June. Most males mature within a two-week period early in the summer, as do some females, but not until mid-August will all females reach adulthood. Most males have died off by the end of the summer; the females commonly live into the autumn during their one-year life span.

Upon becoming sexually mature, the male's lifestyle changes completely. He abandons web building and begins to search for females on their webs. The males are not only looking for mates; they are also searching for food. Without a female's web in which to capture insects, the nomadic adult male has no way to eat.

From late in her final juvenile instar and throughout adulthood, a female Sierra dome spider can expect a new male to visit her web every two to three days. Such visits often last for eight to ten hours, and sometimes even as long as two to five days. Staying in the female's web enables

males to capture prey, find refuge from predators, and with effort and luck, copulate with the resident.

But such visits are problematic for a female. Her ability to reproduce depends on a rich diet, and a nutritious yolk must be provided for each of her eggs. Yet visiting males may gobble up three-quarters of all trapped prey. Unless a female arrives near a struggling insect well before the male, and the prey is small enough for her to carry off easily, the male will promptly grab and consume it himself. Whether they mate or not, males commonly linger to eat and enjoy the web's protection from such daytime predators as wasps and birds.

Although Sierra dome spider males are stronger, larger, and more aggressive than females, they are physically unable to force them to mate. A male's delicate pedipalps, which include the copulatory organs, consist of many bizarrely shaped plates joined by pliant tissues. If a female suddenly twists about or attempts to uncouple too quickly, the male organs can be damaged. Continuous, precise alignment between the male and female parts is necessary, as their genitalia have a close lock-and-key fit during copulation. During intromission, the male sits above the female with his fangs directed away from her, making it impossible for him to retaliate if she becomes uncooperative. Frequent copulating can increase the female's vulnerability to predators, even though her web provides a vibratory early warning system. If the pair is startled and shifts even slightly out of the mating posture, unlocking their sex organs can require nearly a minute—plenty of time for even the most cautious predator to seize them.

The vigor of a female's offspring is probably increased if she selects fit males as sires. From a genetic perspective, the more suitors that visit the female, the better her chances of meeting high-quality males. But how to judge male vigor? A female cannot test males by engaging them aggressively because all males can easily beat her. At the same time, she needs to address the problem of males stealing her prey.

One tactic for dealing with these issues is used by the female just before she becomes mature: pitting male suitors against each other. Females more than five days from maturation stringently

A large fly has blundered into a female dome spider's web, but a visiting male has beaten her to the prize. The female, at left, tentatively pokes the male for stealing her dinner, but stops short of attacking him.
Photographs by Paul Watson

avoid close contact with all males. Then, two to five days before reaching sexual maturity, she begins to advertise her upcoming final molt by staying close to any visiting male and allowing him to probe her body with his legs and pedipalps. If the young female avoids him, the male will depart within a few hours, leaving the female alone until the next male arrives. However, when a male finds a receptive young female, he attempts to win and maintain exclusive possession of her body and web until she matures. Guarding by the male is therefore constant. No male leaves the web of a receptive immature female unless he is forcibly kicked out by a rival. The resultant fights between males eventually lead to a well-tested "champion" on the web. This male becomes the female's first mating partner and usually fertilizes more eggs than any males that come after him.

This mate selection tactic requires many continuous days of male presence in the web; although this means heavy looting of the larder, it comes just at the time that is least damaging to the female's production of eggs. Female spiders normally fast just prior to molting, so the excess food consumed by guarding males during their several days of combat is less of a loss. How far in advance of sexual maturation and fasting a female begins advertising seems to depend on how well she is nourished; a longer period means that more food is sacrificed, but it also means that more males will have time to find the web and contend for her.

The timing of an immature female's receptive behavior seems to have evolved as a trade-off between foraging costs and the genetic gain of having many males vie for first mate status. After their first mating, females never again rely on fights between males to determine sires for their offspring. Perhaps the constant upkeep of a male guard is no longer affordable, as he uses up most of the available food.

Dome webs are supported by a network of fine threads that are difficult for a flying insect to see. When a fly or mosquito hits this superstructure at full speed, it falls, dazed, onto the dome. Alerted by the vibrations, a spider rushes over along the dome's underside, bites the prey, then pulls it through the web. Because the web is not sticky, the spider must seize the insect quickly or it will recover and escape.

Combat between males is not a fail-safe test for the best sire, however. If strong males happen not to show up during the young female's advertisement period, she may get merely the best of a bad lot. A web located near the edge of a population will draw fewer males. If the female matures late in the breeding season, most males may have already been killed in fights or by predators.

If combat between males is not an economical option, the female adopts an alternative method for selecting males with stamina, vigor, and physical coordination: she chooses the best copulator. A suite of adaptations allows her to separate the sex act from fertilization.

First, already mated females often attempt to persuade unwanted males to depart by a forceful, rhythmic web plucking that signals she is not interested in sex. If the female web-plucks, some males curtail their visits by two to three hours; others leave immediately. Still, many males persist; they may want the web's protection from predators or need food so badly that the female's sexual receptivity does not matter. Under these circumstances, however, a female makes copulation and courtship so demanding that the male is unable to compete with her for prey.

A male's pedipalps are not connected to the sperm-producing organs; he must first build a silk platform, or a sperm web, ejaculate onto it, and then draw the semen into his small copulatory appendages. When male Sierra dome spiders enter female webs, their pedipalps are empty. When a pair has been copulating for some time, the act is interrupted so that the male can fill his organs with sperm.

Although matings that eventually result in insemination may last two to seven hours, sperm is transferred only during the final thirty to forty minutes. Thus, most of the time spent mating consists of intromissions that cannot result in sperm transfer—hundreds of brief couplings performed continually over several hours. Each intromission is followed by withdrawal of the pedipalp, grooming it with the mouthparts, one to five seconds rest (a crucial area of variation among males); and then reinsertion of the same or the opposite pedipalp. Males strive to achieve high rates of coupling and uncoupling, and vary substantially in energy use during copulatory courtship. This summer we discovered that, in some males, the working metabolic rate could rise to seven times the resting rate. This is about as hard as a spider can work.

Both body size and intromission rate during copulatory courtship influence the fertilization success of secondary mates (those who become the second, third, or fourth mates of the female). The female chooses a sire for large body size, which my current research suggests predicts the brute strength and metabolic efficiency a male can pass on to his offspring. But she also chooses

those that demonstrate high copulatory vigor, which seems to be associated with their speed in summoning high energy for fighting or capturing difficult prey.

Copulation is consistently demanding for the male, but requires little activity of the female. Consequently, she can remain more alert to capture prey, which requires much quicker responses than the male can muster during mating. Since each intromission by the male lasts only two to three seconds, females can dash off to capture prey in the midst of copulation. While females take only 30 percent of the web's prey during other phases of courtship, during copulation they can grab as much as 80 percent. Females that do capture prey during mating seldom show any interest in resuming copulation until their meal is consumed.

Although more work is needed to be certain, dissections suggest that a female "chooses" which male sires her brood by opening or closing off her sperm-receiving ducts, thereby controlling fertilization of the eggs. How can we know whether females retain the sperm of one male or many, and which males end up being the sires of her brood?

I arrive at my study site with two assistants at the beginning of the summer, when all the spiders are immature. Then we select forty or fifty females on their webs and mark them. One of us visits every web every daylight hour for the entire summer. (The spiders do not mate at night.) We see all the males they mate with and monitor their foraging success hourly. Finally, we collect the successful males immediately after copulation, as well as the rejected suitors, and superfreeze them in liquid nitrogen. Eventually, we do the same with the female and her offspring.

In the laboratory, we analyze subtle, heritable variations in the structures of the spiders' metabolic enzymes, noting those that are unique to each individual. Using these biochemical markers, we can estimate the percentage of offspring that each male has sired. We can even tell how many different males have had their sperm utilized by the female, and which one she has chosen to be the principal sire of her brood.

In any sexual species, males and females must cooperate to reproduce. Much of the Sierra dome spiders' behavior, however, involves little cooperation and a good deal of conflict. Females set up a situation in which males compete with one another to perpetuate their genes and for their very lives—a contest it would be in their interest to avoid altogether. Females have evolved the equipment to dominate the ultimate decision as to which males will sire the spiderlings. And in their demand for long, arduous copulatory courtship, which simultaneously tests the male and reduces his ability to steal prey, the females have evolved an elegant solution to the dual problems of sire selection and foraging efficiency.

Two males, with their pedipalps extended, square off to do battle for an egg-laden female (topmost spider). Sexually mature females that remain unmated for a least a week will soak the web with a male-attracting chemical. In this case, the first male to enter the dome had begun to tear the web silk in an unsuccessful attempt to prevent other males from finding the female. She will have to repair the bunched silk at top right.