Finding Brown's Peony a Sweet Attraction

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Brown's peony flowering in open prairie near the forest edge. Photo by Nan Vance.

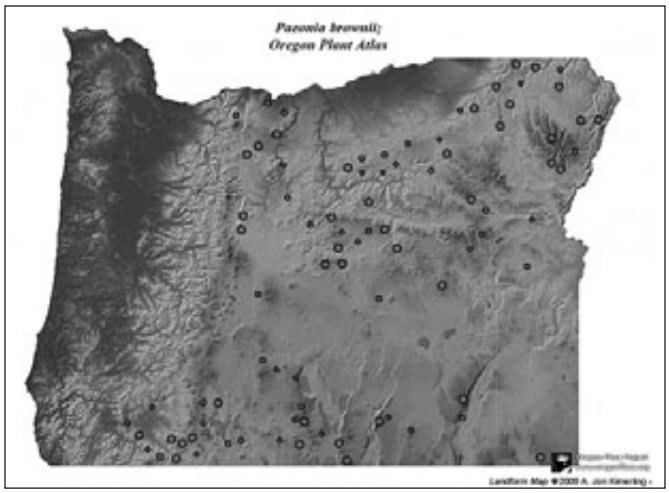
I first encountered Brown's peony (*Paeonia brownii*) with its verdant, lavender-tinged leaves and elegantly nodding maroon flowers growing among bitterbrush and bunchgrass on the eastern flank of the Oregon Cascades. My first thought was "What is a plant like you doing in a place like this?" It would be natural to visualize this native wild peony as a centerpiece in a formal Chinese garden complete with a Koi pond. Perhaps my vision was not that misplaced, considering that most peonies are of Eurasian descent. Asians have venerated the cousins of this peony throughout recorded history for their symbolism, floral beauty, and healing power.

Today the floral beauty of cultivated peonies is universally celebrated in gardens and the arts. Breeders carefully control pollination and propagation to produce a wide variety of floral types. Although our native peony is less showy, it is as hardy and long-lived as its wild relatives of the Eurasian steppe. Many of the Eurasian peony species are threatened in the wild by habitat loss and illegal extraction (Page 2005), but Brown's peony does not seem to be under those same pressures; at least it is not yet the target of a nursery trade. It is surprising how little we know about this species, especially its flowering, pollination and seed production.

Distribution and Habitat

Except for two species, all members of *Paeonia* are Eurasian. California peony (*P. californica*) and Brown's (or western) peony are indigenous to western North America and, like their wild Eurasian relatives, are adapted to habitats with cold winters and warm to hot summers (Page 2005, USDA 1988). Stebbins (1938) suggested Brown's peony was a relict of mesic forests that were once widespread in the northern hemisphere during the Tertiary Period (now Paleocene-Pliocene). He postulated that its populations shrank as the climate warmed, offering as evidence unsuccessful flowering and aborted buds in populations at the southern limit of its range.

The range of Brown's peony spans the interior Northwest, extending from southern British Columbia to the Sierra Nevada in California and east to Wyoming and Utah where it is rare (Hitchcock *et al.* 1964). Its range does not overlap that of California peony, a south-central California endemic that is limited to chaparral and coastal sage scrub in the southern part of the state (Stebbins 1938). In Oregon, the range of Brown's peony extends from the eastern slopes and foothills of the Cascade Range to the Blue Mountains and Owyhee uplands. It extends west of the Cascades only in southern Oregon where it reaches the Siskiyou Mountains.



Distribution of Brown's peony in Oregon. Map courtesy of the Oregon Atlas Project.

Brown's peony thrives in cool, fir-and-aspen communities at middle to high elevations (up to about 8,000 feet), but also persists as scattered individuals in ponderosa pine-dominated forests, open bunchgrass-dominated prairies and dry, sagebrush steppe (USDA 1988). Throughout most of Oregon, Brown's peony is often found in or near seral forest habitats that are prone to frequent wildfire (Agee 1994).

> *... there every man is a physician, wise above human kind; for they are of the race of Paeon. -Homer*
> *Paeonia* is the sole genus in the family Paeoniaceae. The peony is named after Paeon (also Paean) who, according to Greek mythology, was a student of Asclepius, god of medicine and healing. Apollo's mother instructed Paeon to obtain a magical root growing on Mount Olympus to soothe the pain of women in childbirth. When Asclepius became jealous and threatened to kill Paeon, Zeus saved him by turning him into the peony flower.

Description

Brown's peony is a long-lived perennial with branching stems that sprout from buds on its fleshy roots (in the horticultural trade, peony roots are often inappropriately called tubers or bulbs). The often reddish stems bear glabrous, sometimes deeply dissected leaves that are dark green on the upper surface and a lighter, grayish green on the underside. The leaf margins are often purple-tinged, especially in early spring. The solitary bisexual flowers are terminal on the main branches. The greenish-purple bud is globose and the nodding flower is bowl-shaped. The five to six persistent sepals are cupped early on, but later reflex. The five to ten petals are brownish maroon and yellow-tipped at the margins; they senesce and detach when flowering ends. Mounted on the floral axis within each perianth is a ring of dozens of yellow stamens, topped by yellow anthers that open lengthwise. The stamens encircle 2 to 6, glabrous, yellow-red carpels, each having a short style surmounted by a curved stigma. A fleshy disc that encircles the base of the ovaries has greenish-yellow lobes that produce large quantities of nectar. Once the ovules are fertilized, each ovary develops into a several-seeded fruit called a follicle. The seeds are round, yellowish-tan to black, large (a quarter inch or more in diameter), and often fewer than twelve per flower (Hitchcock *et al.* 1964). Peony plants vary in size depending on location and microhabitat; they may appear tall and leggy in the shade or short and spreading in full sunlight. Although long-lived, plants will diminish in size and not flower if conditions are unfavorable but may survive in that state until conditions change (Page 2005).

Observations of Flowering at Three Locations

In the past decade, I have had the good fortune to become better acquainted with Brown's peony through partnering in a study of its flowering and pollination at a site in eastern Oregon and through my own observations at two other locations.

The location of the flowering and pollination study was on the scabland of a shield volcano at about 3,500 ft. elevation within the 6-million-acre Blue Mountains Ecological Province in eastern Oregon. Here, in a mesic-to-xeric bunchgrass prairie adjacent to a coniferous forest, about 300 individuals were scattered in a mixture of grasses, broadleaf herbs, and shrubs. Insect-pollinated species associated with the Brown's peony included redstem ceanothus (*Ceanothus sanguineus*), wild rose (*Rosa nootkana, R. gymnocarpus*), snowberry (*Symphoricarpos albus*), monkshood (*Aconitum columbianum*), balsamroot (*Balsamorhiza sagitatta*, *B. hookeri*), ragged robin (*Clarkia pulchella*), hairy clematis (*Clematis hirsutissima*), *Delphinium* sp., Wyeth buckwheat (*Eriogonum heracleoides*), desert parsley (*Lomatium dissectum, L. triternatum*), sulphur lupine (*Lupinus sulphureus*), *Penstemon* spp., varileaf phacelia (*Phacelia heterophylla*), cinquefoil (*Potentilla glandulosa, P. gracilis*), sagebrush buttercup (*Ranunculus glaberrimus*), American vetch (*Vicia americana*), and mulesear (*Wyethia amplexicaulus*). The peony colony at this site flowers from mid April through mid May.

Open prairie at the Blue Mountains site in eastern Oregon; Brown's peony in foreground. Photo by Nan Vance.

While conducting a different study, I observed a Brown's peony colony on Green Ridge, a flat-topped ridge at about 3,300 ft., on the eastern flank of the central Oregon Cascade Range that drains northward into the Metolius River. Over 100 widely scattered individuals grew within the perimeter of a wildfire that had burned in 2002. The plant community at this location was a ponderosa pine/bitterbrush/Idaho fescue (*Pinus ponderosa*/*Purshia tridentata*/*Festuca idahoensis*) association. Under the fairly open pine canopy,

numerous shrubs and forbs flowered concurrently with the peony: prostrate ceanothus (*Ceanothus prostratus*), greenleaf manzanita (*Arctostaphylos patula*), Carey's balsamroot (*Balsamorhiza careyana*), dwarf hesperochiron (*Hesperochiron pumilus*), woodland star (*Lithophragma parviflora*), chocolate lily (*Fritillaria lanceolata*), and two desert parsleys (*Lomatium triternatum* and *L. nudicaule*). Perhaps because of the recent wildfire, the peony plants had been heavily browsed. Brown's peony began flowering in late April and continued through May. In late August I gathered about 50 seeds from several plants that successfully bore mature fruit, although not all seeds were well developed.

Brown's peony browsed by a large ungulate, presumably elk. Photo by Nan Vance.

In 2007 I came across Brown's peony growing on Puffer Butte, above the Grand Ronde River in the foothills of the Blue Mountains a few miles north of the Oregon border in Washington. There, I found scattered peony plants growing at the edge of a mixed ponderosa pine/Douglas fir forest and into an adjacent open meadow at about 4,600 ft. on a south-facing slope. The bunchgrass opening, dominated by Idaho fescue and bluebunch wheatgrass (*Pseudoroegneria spicata*), was punctuated by brilliant flowering herbs and a few scattered pine trees. At this higher elevation, Brown's peony and other herbs normally flower later than at the other two sites, from mid-May to mid-June, when moist soil and warm temperatures favor rapid growth and maturity. Other herbs flowering at that time included sicklepod rockcress (*Arabis sparsiflora*), arrowleaf balsamroot, yellowbells (*Fritillaria pudica*), ballhead waterleaf (*Hydrophyllum capitatum*), scarlet gilia (*Ipomopsis aggregata*), silky lupine (*Lupinus sericeus*), *Lomatium* sp., bluebells (*Mertensia oblongifolia*), shootingstar (*Dodecatheon* sp.), spreading phlox (*Phlox diffusa*), and larkspur (*Delphinium nuttallianum*) Peonies sheltered by the forest were typically robust, with red stems as large in diameter as a garden hose, and usually produced large fruit packed with seeds In contrast, fruits of unprotected peonies hugging the ground in the south-facing prairie shriveled and failed to develop. It appears that on an exposed and windy aspect these plants are challenged to produce mature seeds when dry soils and hot temperatures arrive too early in the season.

At all three locations, Brown's peony was among the earliest flowering species, occasionally flowering when it was either snowing or snow was still on the ground. All flower buds were terminal and appeared before the leaves had fully expanded. As the buds began to open, I could see the stigmas and a few closed anthers through the sheen of clear viscous nectar. During the first several days of anthesis, the petals retracted enough to expose the receptive stigmas while occluding the anthers which had not yet dehisced or shed pollen. Stigmas were receptive for only about two days, during which time a few anthers had begun to shed pollen.

Pollen was released progressively over a span of roughly two weeks, beginning with stamens closest to the ovaries and continuing outward centrifugally; each day several of the 60 to 90 anthers dehisced, shedding thousands of pollen grains. Within a colony, not all flowers opened at the same time, so flowering continued for about a month. The lobed disc that rings the base of the carpel secretes nectar throughout the flower's lifetime from the beginning of bud opening until the petals fall off. At any one time, only three to four out of the dozen or so lobes secrete nectar (Peter Bernhardt, pers. comm.). The yellowish fleshy lobes shrivel when flowering is over and nectar is no longer being secreted. At the same time the three to five ovaries with developing seeds swell and elongate. At the time of fertilization each ovary typically contains 19 to 20 ovules, of which about 20% develop into seeds (Peter Bernhardt, pers. comm.). Meanwhile, the senescent petals fall off the flower that hangs pendant on the curved stem. The elongated stems become increasingly decumbent as the heavy follicles swell with seeds. By late summer to early fall, they bend to the ground and the dark, leathery follicles split to release large brown seeds.

A Few Good Seeds

Of the 50 mature seeds I collected at Green Ridge, 92% were filled and appeared viable. Fully developed seeds are plump and contain a starchy white endosperm and a tiny embryo at one end. Seeds vary in size, ranging from 0.2 to 0.5 inch at their widest diameter.

Partially shaded plants of Brown's peony with stout purple-red stems and buds in early spring at the Puffer Butte location. Photo by Nan Vance.

Open flower, revealing stigmas, anthers and partially hidden lobes of the nectariferous disc. Photo by Nan Vance.

Seeds are food for rodents as well as arthropods, so animal dissemination is possible (Schlising 1976). Although birds and rodents travelling with seeds may drop or bury them, I saw no direct evidence of that; instead, I noted seedlings close to the parent plants. Sometimes seeds from a single flower germinated together to form a small cluster.

The seedling foliage also can be subject to herbivory, which results in considerable mortality. In November I planted 22 of the seeds I had collected earlier at Green Ridge in marked plots in the general vicinity of the parent plants. Most of the germinants (17) had emerged by early March of the following year when snow was still on the ground. The long cotyledons were large and almost fleshy. I followed the seedlings' progress that spring and noted that many of the developing young leaves were eaten by insects to the extent that some seedlings were reduced to stubs. I do not know if any survived. I optimistically surmise that since the peony is long-lived, replacement does not have to be a frequent occurrence, and it doesn't appear to be. Herbivory was common at the Green Ridge location and predation of flowers and fruit (at least the years I visited) occurred at all three locations I visited.

Insect Visitors and Pollinators

Based on observations at all three sites, Brown's peony exhibits floral traits that are consistent with a generalist pollination system most likely dominated by flies. The unspecialized flowers attract a diversity of visitors, some of which may serve as pollinators, which in turn ensures that pollen is transferred, even if the abundance of particular pollinators fluctuates over time.

At the Blue Mountains reserve study site, the most frequent insect visitors that carried pollen of Brown's peony were large flower flies and predatory wasps. The most common were the Bombus-mimicking fly, *Criorhina caudata* (Syrphidae), and the wasp queens, *Dolichovespula arenaria* (Vespidae) and *Polistes aurifer* (Polistidae). Six species of wasps represented almost half of the visitors recorded at that location. The wasps tended to visit flowers from late morning through the afternoon after the temperature had warmed a bit. On the other hand, like other large, hairy syrphid flies, *C. caudata* actively foraged for nectar in the morning hours at the Blue Mountains site from April until the beginning of the first week in May, even on the coldest days (32°F).

Female solitary bees in the genera *Andrena* and *Lasioglossum* (*Evylaeus*) appeared to forage for nectar in mostly staminate-phase flowers, probably because they often visited the peonies late in their flowering cycle. While bees forage for nectar they accidentally pick up pollen grains. A diverse mix of pollen grains on these bees suggested that they frequented a variety of co-flowering shrubs and herbs and visited the peony flowers only for nectar. In the spring, females may take nectar back to the nest to mix with the pollen to feed the larvae; or they may stop for nectar to renew their energy while returning to their nest after gathering pollen (the bee equivalent of stopping for a double latte on the way home from work). Although bees appeared to visit Brown's peony at the Blue Mountain study site after flowers petals opened during

The fully developed fruit of Brown's peony beginning to ripen. Photo by Nan Vance.

A cluster of peony seedlings that germinated where the seeds fell from the fruit. Photo by Nan Vance.

the staminate phase, at Green Ridge and Puffer Butte I observed solitary bees visiting peony flowers throughout their lifespan.

At Green Ridge and Puffer Butte, I observed fewer wasp visits than at the Blue Mountain study site. Mostly flies, bees, and ants appeared to be foraging on the flowers. Although wasps did not appear as frequently as bees at the Green Ridge site, I saw a large (queen) hornet, *Dolichovespula adulterina,* visiting flowers and ingesting nectar; this species is an obligatory social parasite of *D. arenaria* (Greene *et al.* 1978)**.** At Puffer Butte, I found *Bombus*-mimicking and other large flies, medium-sized bees, and large vespine wasps. Ants were more common at both of these locations than they were at the Blue Mountains reserve. Not surprisingly, where large predatory wasp and hornet visits were abundant, the visits of ants were fewer in number; conversely, ants were a frequent flower visitor where wasp visits appeared to be infrequent. Forensic evidence of the predatory nature of Vespine wasps was provided by the *P. aurifer* Peter Bernhardt captured with an ant head grasped in its tarsal claws.

The differences in composition of the insect pollinator groups among the three sites also may reflect their different geography, disturbance history, plant communities, and abundance of co-flowering species. Successfully attracting large wasps and flies does not preclude other generalist insects from functioning as effective secondary pollinators, especially if they aren't visiting flowers at the same time. For such a wide-ranging species as Brown's peony, a flexible pollination system with provision for alternative pollinators provides a buffer against changes in climate and plant and insect communities.

Why Floral Nectar?

Very few species in the genus *Paeonia* secrete floral nectar, yet Brown's peony does. And, unlike the bees and beetles that visit flowers of California peony to collect pollen and nectar (Schlising 1976), insects appear to visit Brown's peony flowers almost exclusively for nectar. Nectar attracts pollinators in early spring when their energy sources are scarce and nutritional needs are great. In fact, nectar may be critical for the survival and reproduction of pollinators at this time of year. For example, wasp queens emerging in early spring can lose up to about one-third of their body weight (Spradbery 1973). At key times in their life cycle, syrphid flies depend exclusively on high-energy nectar. Sutherland *et al*. (1999) reported that they appeared to select flowers with the greatest nectar volumes and highest sugar concentrations.

The sugar concentration of the nectar ranged between 20 and 30%, which is within the range desired by insect nectar feeders (Nicolson 1998). Both major components of peony nectar (sugar and amino acids) are important nutrients for wasp and fly pollinators (Baker and Baker 1986); for example, proline is required by wasp larvae prior to pupation (Hunt *et al*. 1998) and is readily metabolized into energy. Amino acids are also an important energy source for syrphid flies (Carter *et al.* 2006).

There was ample evidence at the Blue Mountains reserve that the wasp queens gorged on nectar during the spring months. Euthanized wasps leaked nectar when pinned and nectar volume

A large hornet queen (*Dolichovespula adulterina*) forages for nectar on a partially opened peony flower. Photo by Nan Vance.

decreased drastically in flowers visited by wasps. The wasps kept coming back even as flowers changed their appearance over the flowering period, which suggests that wasps were attracted primarily by scent of the nectar. The native peony's sugary floral nectar is an analogue of the sticky exudate of garden peonies, which would explain why the domestic peonies also have wasps and ants crawling all over them.

Prospect for the Future?

Since my first encounter with Brown's peony years ago, my attachment to this native species has deepened, as well as my understanding of its relations with the insects that depend on it for survival and in turn, contribute to its survival. Our peony is not a prolific seed producer, and it may not need to be because, as a long-lived perennial, it need only replace itself occasionally over its lifetime. Additionally, because of food reserves stored in its fleshy roots, it has the capacity to resprout after fire and herbivory which helps established colonies to persist (Page 2005). If disturbance of these habitats exceeds our peony's resilience, low fecundity could make its populations vulnerable to decline.

So, the next time you see our native peony and its lovely nodding flowers filled with nectar, think of a plant of great generosity rather than extravagance. Its cold-hardy flowers furnish nutritious, high-energy food for native insects that brave the vagaries of early spring in the interior Northwest. We are fortunate to have habitats that support populations of our native Brown's peony, an elegant denizen of Oregon's dry prairies, east side forests and Siskiyou Mountains.

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Nan Vance retired from the USDA Forest Service Pacific Northwest Research Station after 20 years. At the Corvallis Forestry Sciences Laboratory she led a research team that worked in restoration, conservation and sustainable management of native forest plants of the western region. Her primary research emphasis in plant physiological ecology, reproductive and conservation biology of native plants of the Pacific and Intermountain West resulted in over 40 publications. She also served as a Courtesy Graduate Faculty member in the College of Forestry and Plant Physiology Program at Oregon State University. Trained as a plant physiologist, she became interested in pollination biology in the past decade. This interest has continued after retirement through her photography and personal study of flowering plants and their insect associates in Oregon as well northcentral Idaho and southeastern Washington, where she spends her summers.