

REPRODUCTIVE BIOLOGY OF *DARLINGTONIA CALIFORNICA*

By

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ABSTRACT

Reproductive Biology of *Darlingtonia californica* Torrey 1853

by

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Various aspects of the ecology and natural history of *Darlingtonia californica* Torrey 1853, populations in northern California were studied as they relate to the species' reproductive biology. Experimental investigations of the breeding system to estimate natural levels of selfing and outcrossing rates were performed by measuring seed set in six treatments. Seed set in an open-pollinated control treatment was quite high and almost entirely the product of cross-pollination. Seed set in the treatment involving extra pollen added through hand-pollination was even higher, which suggested that there was competition for limited pollinator services and that seed set was pollinator, not resource, limited. Seed set was lowest in the treatment where pollinator access was denied, indicating that while the species is not autogamous, it is marginally self-compatible. The pollinator-exclusion treatment suggests that the species sets few to no seeds in the absence of pollinators. However, extended field examinations of flowering *Darlingtonia* populations, totaling over 120 hours, failed to detect any pollinators visiting the species. An as yet undescribed, yellow-petaled flower variety was discovered in the course of field studies, and found to be similar to typical purple-petaled flowers in seed set, peduncle height, number of bracts and number of anthers. An extensive search of the literature on *Darlingtonia californica* was conducted and resulted in an annotated bibliography consisting of 60 articles, books and reports. To my knowledge, it is the most complete conducted to date.

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INTRODUCTION

Species Description

Darlingtonia californica Torrey 1853, the California pitcher plant, is a monotypic member of the Sarraceniaceae, a small family of carnivorous plants. The family includes the genera *Heliamphora* of South America and *Sarracenia* of the southeastern United States. As *Darlingtonia californica* is a monotypic species, I will herein refer to it simply as *Darlingtonia*.

Darlingtonia is the sole representative of its family in the United States found west of the Mississippi. It is distributed from the northern coast of Oregon to California's central Sierra Nevada. However, the highest density of documented sites is found in northwestern California in the Klamath, Siskiyou, Shasta and Trinity Mountains (Debuhr, 1973). It ranges in altitude from near sea level in Oregon to 8,100 feet in the Trinity Alps of California. Currently, it inhabits a total of 180 documented sites in 16 counties (Rondeau, 1995).

Although this species is found over a broad range of altitudes and latitudes, its specific habitat requirements are met in only a small portion of its range. Like other carnivorous plants, *Darlingtonia* is restricted to moist, nutrient-poor sites. Generally, the species is found on serpentine-derived soils, or on sites irrigated by waters that have flowed through serpentine. It is found primarily along montane creeks and meadows where perennial springs constantly bathe its roots with cold, oxygen-rich waters. Its habitat receives an annual average of 40-60 inches of precipitation (Debuhr, 1973). Sympatric species often include *Hastingsia alba* Durand, bog asphodel (*Narthecium californicum* Baker), *Tofieldia occidentalis* S. Watson, grass-of-parnassus (*Parnassia californica*) (A. Gray) E. Greene and Labrador-tea (*Ledum glandulosum* Nutt.), as well as a variety of lilies, sedges,

ericaceous shrubs, and carnivorous plants including butterwort (*Pinguicula vulgaris* L. ssp. *macroceras* (Link) Calder & Roy Taylor, and sundew (*Drosera rotundifolia* L.).

Reproduction is primarily asexual, by rhizomes, each of which produces several rosettes of insect-trapping pitcher-leaves. The tubular shape of the leaf, which terminates in a forked appendage resembling a snake's tongue, has given the species the colloquial name 'cobra lily.' Each rosette produces a large, solitary blossom on a tall peduncle. *Darlingtonia* is among the earliest spring bloomers in its habitat.

Due to its unique and limited habitat and over-collection by carnivorous plant enthusiasts, it is considered a Federally protected species. The California Native Plant Society includes it on their watch list of species with limited distributions (Skinner and Pavlik 1994).

Literature review

Since *Darlingtonia*'s discovery near Mount Shasta, California, 154 years ago, at least 61 articles, reports, chapters and books have focused on the species. The earliest publication was the original monograph authored by botanist John Torrey in 1853 (Torrey 1853). The species' discovery during the Victorian era's fascination with natural history ensured much interest in the carnivorous plant. Early papers were authored by Gray (1853, 1863), Hooker (1871,1875) and Macfarlane (1889a, 1889b).

Certain aspects of its biology have been studied more intensely than others, particularly the morphology of the pitcher-leaf relating to prey capture and digestion (Adams and Smith 1977, Arber 1941, Canby 1874, Franck 1975,1976, Glosner 1992, Hepburn et al. 1927, Heslop-Harrison 1978, Lloyd 1942, Macfarlane 1889a, 1889b) identification of prey (Austin 1875-1877, Edwards 1876, Joel 1988, Naeem 1988, Rondeau 1995) and identification and ecology of the pitcher-inhabiting arthropods (Edwards 1876, Elder 1993, Naeem 1988, Naeem and Dushek 1985, Nielsen 1987, 1990).

Fewer studies have focused on other parts of the species' morphology. Pollen structure was investigated by Debuhr (1973) and Thanikaimoni and Vasanthy (1972), chromosome structure and number by Bell (1949) and seed structure by Debuhr (1973), Dwyer (1983), and Gray (1863). The structure and function of the blossom and fruit capsule were investigated by Canby (1874), Debuhr (1973) and Torrey (1853).

Papers on the species' discovery include Clark 1990, Gray 1853, Viola and Margolis 1985; on distribution (Debuhr 1973,1974, Rondeau 1995), and evolution (Mellichamp 1983). Taxonomic and phylogenetic relationships have been investigated by Debuhr (1975, 1977), Franck (1976), Thanikaimoni and Vasanthy (1972), and Torrey (1853).

Habitat characteristics and plant associates have been briefly reported by Cheatham (1976), Fowlie (1982), Keeler-Wolf (1982, 1986), Knight and Howell (1970), Lutz and Magi (1980), Pickart and Berg (1986) and Sawyer (1986), Sawyer and Keeler-Wolf (1996) and Whipple (1981).

Reports on *Darlingtonia*'s rare plant status and the current and potential threats to its habitat have been authored by the California Department of Fish and Game (1995), Horner (1976), Oregon Natural Heritage Program (1995), Skinner and Pavlik (1994) and Stansell (1980).

Books on carnivorous plants containing in-depth chapters on *Darlingtonia* have been written by Juniper et al. (1989), Schnell (1976), Slack (1988), Rondeau (1995), and Lloyd (1942).

In contrast, little has been published on the species' natural history, especially in relation to reproductive and pollination biology. For example, Juniper (1989) noted that "few workers have made even the briefest of comments on the pollination of carnivorous plants, although it is generally considered, with incomplete evidence, that all carnivorous plants are insect-pollinated." Regarding *Darlingtonia* specifically, Juniper added that "whether *Darlingtonia* is self-pollinated or cross-pollinated will have to remain a mystery".

Those who have delved into this subject area (Austin 1875-1877, Debuhr 1973) have done so briefly, without any quantitative field experiments. Few have studied floral anatomy (Debuhr 1973), and none has looked at gross morphology or flowering phenology, aspects of *Darlingtonia*'s biology which are investigated in this study. Elder (1994) authored the preliminary results of the following study.

Objectives of study

The purpose of this study was to gather base-line data on *Darlingtonia*'s reproductive biology. Specifically, this study addressed the following questions:

1. Does *Darlingtonia* effect sexual reproduction by cross-pollination or self-pollination?
2. If found to reproduce by cross-pollination:
 - A. Who are the most common and effective pollinators?
 - B. Is seed set limited primarily by resources or by pollinator visitation?
 - C. Do pollinators discriminate against the rare yellow-petaled flower variety?

My primary objective was to answers the above questions by testing the null hypotheses that there were no significant differences between the mean number of seeds matured per fruit between the following pairs of treatments:

1. Control and pollinator-excluded blossoms.
2. Control and emasculated blossoms.
3. Control and hand-pollinated blossoms.
4. Control and yellow-petaled blossoms.
5. Emasculated and emasculated + pollinator-excluded blossoms.

During my field work, I discovered a yellow-petaled variety of *Darlingtonia*. Thus, a second, and related objective became to compare its general floral morphology with that of the typical variety and determine if pollinators discriminated against the rare color as evidenced by lowered seed set.

The third objective of this study was to conduct a complete literature search on *Darlingtonia* and to compile an annotated bibliography.

DESCRIPTION OF STUDY SITES

Study site #1. Grouse Ridge. Nevada County, California

This study site, herein referred to as Grouse Ridge, is near the southern edge of *Darlingtonia*'s range. It is in Nevada County, California, approximately 30 air miles due east of Nevada City, near Lake Spaulding, on the north-facing slope of Grouse Ridge at 5,700' (Figure 1). Due to its fragile wetland characteristics and location on private property, the site's exact location will not be cited.

Unlike many locations where *Darlingtonia* grows, this site is not located directly over serpentine. However, the site may be irrigated by waters that have flowed through subsurface intrusions of serpentine, a not uncommon occurrence.

The study site is located in a half-acre meadow, through which flows a perennial spring that drains into the south fork of the Yuba River. Although *Darlingtonia* is the most abundant species, it shares the site with a rich and diverse flora, including the carnivorous round-leaved sundew (*Drosera rotundifolia* L.); the saprophytic naked broom-rape (*Orobanche uniflora* L.) and a wide assortment of orchid and lily species. (See Appendix I for species list).

The meadow is ringed by a thicket of mountain alder (*Alnus incana* (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung) and scattered lodgepole pines (*Pinus contorta* Loudon ssp. *murrayana* (Grev. & Balf.) Critchf.), which in turn is surrounded by a second-growth yellow pine forest typical of this altitude. This forest consists of sugar pine (*Pinus lambertiana* Douglas), ponderosa pine (*Pinus ponderosa* Laws.), white fir (*Abies concolor* (Gordon & Glend.) Lindley), and incense cedar (*Calocedrus decurrens* (Torrey) Florin), with an understory of mountain whitethorn (*Ceanothus cordulatus* Kellogg),

sierra gooseberry (*Ribes roezlii* Regel), chinquapin (*Chrysolepis sempervirens* (Kellogg) Hjelmq.) and bracken fern (*Pteridium aquilinum* (L.) Kuhn var. *pubescens* L. Underw.).

Annual precipitation at the nearby Bowman Dam weather station for 1993 was 66.71 inches, a -.24 departure from the thirty year average. Annual average temperature is missing from this station. However, annual average temperatures at surrounding stations are well within the thirty year average (U.S. National Climatic Data Center 1993).

Study site #2. Mount Eddy, Trinity County, California

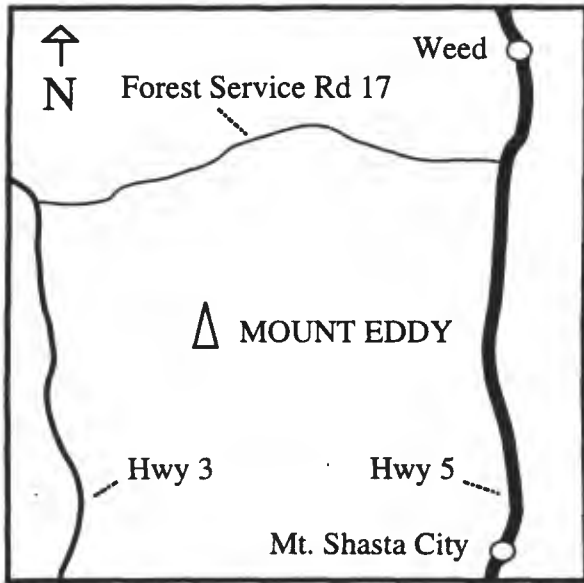
This study site, herein referred to as Mount Eddy, is near the center of *Darlingtonia*'s range, where the highest density of sites are found. The site is located in Trinity County, California, approximately 20 air miles due west of Mount Shasta on the western slope of Mount Eddy, which at 9,025' is the highest summit in the Klamath Mountain region (Figure 1).

The habitat for *Darlingtonia* is quite extensive at this site, but I limited my observations to the northwest-facing meadows along Deadfall Creek, a tributary of the upper Trinity River, extending from 6,000' to 8,000' in elevation. The meadows support a rich and diverse flora whose characteristic species include *Hastingsia alba* (Durand) S. Watson, *Tofieldia occidentalis* S. Watson ssp. *occidentalis*, monkshood (*Aconitum columbianum* Nutt.) and white-flowered bog-orchid (*Platanthera leucostachys* Lindley). The meadows are found scattered within the open forests characterized by Whipple (1981) as white pine woodlands, and are composed primarily of western white pine (*Pinus monticola* Douglas), with scattered white fir (*Abies concolor* (Gordon & Glend.) Lindley), foxtail pine (*Pinus balfouriana* Grev. & Balf. ssp. *balfouriana*), whitebark pine (*Pinus albicaulis* Engelm.), and shasta red fir (*Abies magnifica* Andr. Murray var. *shastensis* Lemmon).

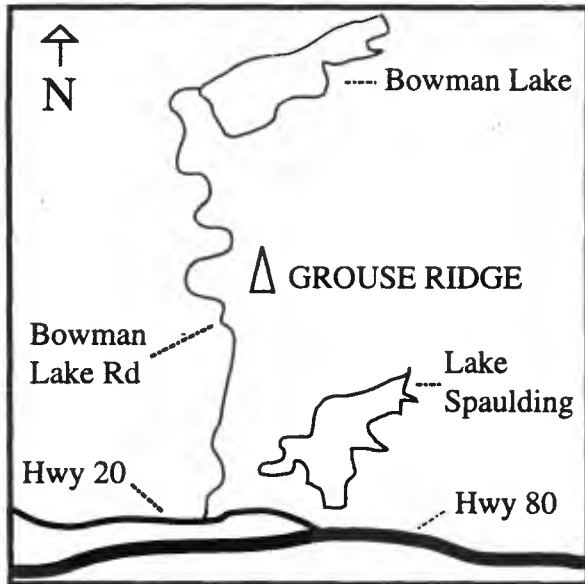
The understory includes *Arctostaphylos nevadensis* A. Gray, huckleberry oak (*Quercus vaccinifolia* Kellogg), common juniper (*Juniperus communis* L.), and mountain gooseberry (*Ribes montigenum* McClatchie). See Appendix II and Whipple (1981) for more complete floristic surveys of the Mount Eddy region.

Annual precipitation at the nearby Callahan weather station for 1993 was 20.84 inches, a -.36" departure from the thirty year average. Annual average temperature was 48.9 F., a -1.6 F. degree departure from the thirty year average (U.S. National Climatic Data Center 1993). Although Callahan is significantly lower in elevation than Mount Eddy, it is located close enough to assume that Mount Eddy also experienced a fairly typical weather year.

B. Mount Eddy. Trinity County, CA.



C. Grouse Ridge. Nevada County, CA.



A. California

Scale: 1" = 10 miles

Figure 1. Location map (A), and site maps: Mount Eddy (B) and Grouse Ridge (C).

METHODS

Methods of choosing study sites

My study sites were chosen for their healthy, relatively undisturbed populations of *Darlingtonia* and their convenient locations near roads and services.

Several factors contributed to the need for two sites instead of one. First, because of the fragile nature of the wetland habitats supporting *Darlingtonia* populations, I wished to lessen my impact on any one site. Second, I did not want to unnecessarily interfere with my long-term plots set up at the Nevada County site (seed set and flowering phenology experiments) while conducting other studies. Third, the differences in blooming seasons between the two sites enabled me to conduct field observations for a longer period, lasting from May to August, 1993. And lastly, I wished to compare the two sites in terms of flower morphology.

Some experiments were conducted in Nevada County, while others were conducted in Trinity County. At Grouse Ridge I performed the following experiments: seed set experiments, study of yellow-petaled blossom, blossom morphology and pollinator observations. At Mount Eddy I performed several experiments but only the pollinator observations are reported here.

I chose to conduct the long term seed set and phenology experiments at Grouse Ridge instead of Mount Eddy because it was more convenient to make the frequent visits necessary for those experiments at that site. The choices of which site to use for the other experiments was purely random.

In order to describe the general botany of the study sites, I identified the major trees, shrubs and herbs found in the vicinity, using Hickman (1993). Lists of these species are found in appendix I (Grouse Ridge site) and appendix II (Mount Eddy site).

Methods for seed set experiments

Experimental investigations on the number of seeds matured per fruit capsule (seed set) were carried out using the following six treatments:

1. Control.
2. Yellow-petaled.
3. Hand-pollinated.
4. Emasculated.
5. Pollinator-excluded.
6. Combined emasculated + pollinator-excluded.

Each was designed to address a separate question on reproductive biology. The control treatment was used to determine the natural seed set in unmanipulated blossoms. The yellow-petaled treatment was used to determine the natural seed set in unmanipulated blossoms which bore yellow petals, a rare and previously unreported blossom color. The hand-pollinated treatment, consisting of blossoms to which extra pollen was added by hand, in addition to allowing natural pollination, was used to determine whether seed production was pollinator-limited.

The emasculated treatment, consisting of blossoms whose pre-dehiscent anthers were removed, was used to determine whether seed set would be lower than the control treatment, suggestive of a breeding system that included self-pollination. The pollinator-excluded treatment, consisting of blossoms protected from pollinator visits by means of draw-string bags, was similarly used to determine breeding system by observing if seeds could be produced by self-pollination in the absence of pollinators. The combined emasculation and pollinator-exclusion treatment was a combination of the two previously described treatments, and was used to determine if the bags were indeed effective in

preventing pollinator visitations, for any resultant seed production would obviously be due to pollinators slipping through the bags to fertilize these blossoms.

Seed set experiments were performed at Grouse Ridge from June- August, 1993. Choosing the treatment blossoms was conducted from June 5–12. This timing was chosen to coincide with the beginning of the growing season, for the snow had recently melted and the blossom buds were just beginning to emerge from the centers of each rosette of pitcher-leaves. Over this eight-day period, I was able to find a sufficient number of buds that met my age requirements. Choosing blossoms at the correct bud stage was especially critical in the pollinator-excluded, emasculated, and emasculated plus pollinator-excluded treatments, where it was imperative to ensure no pollinators had visited the blossoms before bagging.

My experimental design and methods were inspired by those carried out by Schemske et al. (1978) and followed their protocol, as well as those outlined by Dafni (1992). I chose and labeled 127 blossom buds to be used in the six treatments (20 for each treatment except the pollinator-excluded and hand-pollinated treatments). For the pollinator-excluded treatment I chose 30 blossoms because I anticipated a greater mortality rate because of the bags and knew that the anticipated small seed set would require a larger sample size for statistical purposes. For the hand-pollination treatment I chose 17 blossoms due to the fact that the average blossom bears 17 anthers (personal observation) and I required that all treatment blossoms be pollinated by the same donor blossom to reduce genetic variability.

The total sample size of 127 blossoms was determined by the fact that only a certain number of buds was at the correct stage of development, old enough to endure handling, labeling and bagging, yet young enough to have not yet opened. The advantage of a small sample size was that it reduced my physical impact to the site, and since the percentage of manipulated blossoms was small compared to the population size, pollinator behavior would not be adversely effected. Since the site is large, nearly an acre, with an estimated

1,000 blossoms at the height of flowering (personal observation) I felt that my sample size was small enough to be of little ecological consequence, but large enough to provide valid statistical results.

Once I had chosen, flagged and numbered the blossoms, I assigned one of the six treatments to each blossom. For example, one treatment was assigned to blossoms # 1-20, another treatment was assigned to blossoms #21-40, etc. I then attached a numbered label to the peduncle of each blossom indicating treatment number (#1-6) and blossom number (#1-20). However, the yellow-petaled treatment blossoms were chosen in another fashion since there was only a total of 28 and they were dispersed unevenly among the normal blossoms. I randomly chose 20 from the total number that I had previously mapped and identified at the site.

Although my method of choosing which blossom received a given treatment was not entirely random, I had valid reasons for using a more systematic method that I believed outweighed any possible biases in that method. For example, if blossoms of a given treatment were scattered randomly throughout the site, unnecessary trampling would occur while trying to relocate individuals to perform the various manipulations unique to each treatment. Thus, I reasoned that the inevitable trampling of the site from use of the random method would have affected the validity of the results more than the systematic method which I employed. In addition, I found no apparent environmental gradient across the site that could have affected seed set. All of the treatment blossoms were centrally located and within 100 feet of each other, and virtually identical in slope, aspect, exposure and moisture regime.

Once the blossoms were labeled, each was handled differently depending upon the treatment assigned. The control and yellow-petaled treatment blossoms were simply labeled and left to mature unmanipulated.

For the pollinator-excluded treatment, I carefully checked each bud to make sure that it was sufficiently young, having sepals and petals tightly appressed to the ovary, and with anthers undehisced. The bud also had to be large enough, and on a long enough peduncle, to support the weight of the pollinator-exclusion bag. In addition, it had to be young enough to not have been colonized by the ubiquitous spiders found on virtually every mature blossom. If a particular bud was not of the correct age, I chose another. I then covered each bud with a bag fabricated out of 'bridal veil'-a lightweight, white cotton material, around which I'd sewn a drawstring. This bag was fitted loosely around the bud and tied just below the insertions of the sepals on the peduncle. The fabric was light enough to be supported by the blossom and to allow photosynthesis to occur, but of a sufficiently fine mesh (about 1 mm) to exclude any probable pollinator.

Every few days, as the flowers grew, I checked each bag and adjusted it to insure that it was still in the correct position and not tied too tightly. The bag was left on until the sepals and petals began to wither, signaling that the flower had either died or gone to fruit.

For the emasculation treatment, anthers and stamens were removed from each bud prior to maturation. By gently separating the young sepals and petals appressed to the ovary and, using fine, sharp tweezers, I carefully removed each of the stamens (average 17) at the base of the filament's insertion on the ovary. I checked to be sure that the anthers were green and immature, to insure that there was no chance that they had already released pollen onto the blossom's stigmas.

For the emasculated plus pollinator-excluded blossom treatment, I removed all stamens in addition to bagging each bud, using the same techniques described above. This treatment was designed to test whether the bags were effective in excluding pollinators, for any seed set would have had to have been a result of cross-pollination.

The hand cross-pollinated treatments received pollen from natural sources as well as pollen I added experimentally. Since I did not know the exact time the stigmas were receptive to pollen, I hand-pollinated them twice, once on June 23, as the receiver blossoms' anthers were just beginning to dehisce, and again on June 28, as the anthers were drying up, and had finished dehiscing. This procedure virtually insured that the blossoms received enough pollen during the time I believe the stigmas were receptive, that is, from the last few days of anther dehiscence until a couple of days afterwards. I used only one pollen donor blossom on each occasion to pollinate all of the treatment blossoms. This technique served to reduce the genetic variability of the resultant seeds that may have differentially affected numbers of seeds set per capsule. Thus, a total of two donors were used— one on June 23 and a second on June 28, both of which represented typical blossoms and were healthy, with mature pollen. Each was approximately 20 feet away from the treatment blossoms. This distance was chosen as a balance to minimize the possibility that the donor and receiver were closely related (possibly lowering seed set) while ensuring that they were in the same micro-habitat.

The pollen-donor blossom was picked and immediately carried to each pollen-receiving blossom. The pollen was collected by carefully folding back the sepals and petals to expose the stamens. Fine, sharp tweezers were used to grasp the base of the filament and remove the entire stamen intact (in the same manner that I had emasculated the previous pollen-donor blossoms). Next, the anther was gently brushed against each of the five stigmas of one blossom's style. Thus, one of the 17 anthers borne by the donor blossom was used to pollinate one of the 17 treatment blossoms.

In order to insure that no seeds were lost from the maturing capsules before their harvest date (since they could open when I wasn't present), I bagged all blossoms that had not been previously bagged, i.e. the control, yellow-petaled, emasculated, and hand-pollinated

blossoms. Blossoms were bagged once the sepals and petals had withered and the capsule had begun to mature.

On August 10, I harvested the maturing fruit capsules of all treatments. The fruits were collected prior to their dehiscence and so the bags had been a practical but unnecessary precaution. The number of mature seeds per fruit was recorded for all treatments.

Methods of pollinator observations

In an attempt to identify potential pollinators and quantify their behaviors, I made extended observations of plants, blossoms and their visitors throughout *Darlingtonia*'s blooming season. Observations were conducted from April through June, 1992 and April through August, 1993. Most observation hours were accumulated from May through July, 1993 while I was performing the other experiments of this study. Principal investigations were conducted at Grouse Ridge and Mount Eddy, with occasional visits to nearby sites as time allowed.

Observations were made throughout the day, from approximately 9:00 A.M. to 9:00 P.M.; the majority occurred from 10:00 A.M. to 4:00 P.M. These were the hours of greatest insect activity. Little activity occurred earlier or later, presumably because of lower than optimum air temperatures associated with the altitude, and the abundance of cold water running through the sites, that made the seeps colder than surrounding areas. A total of approximately 125 hours were spent in the field, 100 hours at Grouse Ridge and 25 hours at Mount Eddy. The subset of these hours devoted exclusively to pollinator observations was not independently recorded. Except for time spent recording field notes, I believe that during most of this time I was aware of any pollinator activity occurring nearby.

I used several observation methods in my search for pollinator activity on *Darlingtonia*. At regular intervals, I would sit quietly among a patch of flowers for approximately 15

minutes, watching for signs of any insect visitors. I would then move to another nearby patch. I am quite sure my presence had neither positive nor negative effects on insect behavior, since numerous insects were present, flying around and visiting neighboring plant species, seemingly without noticing me.

A second method involved walking throughout a site while examining flowers one by one. Since the flower is functionally tubular, with its reproductive parts hidden, I found it unproductive to simply observe a field of flowers. Instead, I manually spread the sepals and petals which clasp the ovary to inspect for pollinators which may already be inside, such as tiny thrips, aphids or beetles.

My last technique involved simply watching for any potential pollinator activity while I was occupied with other field experiments. For example, over the course of the season while conducting the experiments with seed set, phenology and morphology, I handled hundreds of flowers and was always alert for pollinators. A total of at least 1,000 blossoms were handled at the Nevada County site and 1,300 blossoms at the Mount Eddy site. I used several criteria to differentiate casual blossom visitors from actual pollinators. In general, pollinators are characterized by having behavior and morphology consistent with transporting pollen from the anthers of one blossom to the stigmas of another. Thus, a pollinator visits a number of flowers in succession to gather nectar or pollen and in doing so, effects cross-pollination. In addition, a pollinator is morphologically adapted to carry pollen. Thus, a pollinator possesses some combination of hairs, spines, feathers, etc., to which the pollen adheres during the journey to the next flower. Thirdly, a pollinator must exhibit characteristic pollination behavior to convince one that it is indeed effecting cross-pollination for that species. For example, although butterflies are common, well-known pollinators in many habitats, and even use the blossoms of *Darlingtonia* as resting platforms, the butterfly's behavior does not include foraging from *Darlingtonia* for nectar

or pollen, or flying from flower to flower in a systematic way. Thus, I would conclude that butterflies are not among *Darlingtonia*'s pollinators.

Potential pollinators were captured with an insect net and immediately placed in glass jars containing ethyl acetate-soaked cotton balls, a material commonly used to kill insects (Borror et al. 1989). However, since no clear pattern of consistent visitation was observed among these insects, I determined that the collected insects were not likely to be pollinators after all; thus I did not identify them.

In an attempt to capture elusive and/or crepuscular pollinators that I might otherwise have missed, I applied a glue-like substance to flowers, with the hope that visiting pollinators would be captured. I used a substance called Tanglefoot™, manufactured for gardeners to use to capture and kill garden pests. I chose this brand because of its sticky properties, low toxicity and ease of application. I used a small wooden wand to apply the substance to the stigma, style and ovary of 20 blossoms. I thoroughly checked each blossom for entangled insects during the next 5 days, at which time they began to wither.

Morphological comparison of previously unreported yellow-petaled flower variety with typical purple-petaled variety

I first observed the yellow-petaled flower variety while making an informal visit to the Grouse Ridge site in the summer of 1992. I then searched the literature for any reference to it and found none. When I returned to the site the following summer to conduct my field studies, the yellow-petaled variety was again found blooming in approximately the same area of the seep. On June 22, 1993, at approximately the height of the blooming season, I thoroughly searched the entire site and identified and mapped the population of yellow-petaled flowers.

My discovery of this variety led me to wonder whether it differed morphologically from typical flowers, and if so, whether such differences could account for possible pollinator discrimination. Thus, I described and compared the gross morphology of the two varieties. Except for the yellow petals, it would have been hard to tell the two apart, for they did not seem to differ in any readily observable way.

I chose the most distinctive morphological variables to quantify: flower height, number of anthers and peduncular bracts. Additionally, these characters seemed to be those that would most likely affect pollinator visitation. Seed set was also compared as described in the previous section.

These morphological comparisons were carried out only at the Grouse Ridge site, for this is to my knowledge the only site that supports this variety. The date was June 22, at the height of the blooming season when most of the flowers were mature. I chose for measurement all 28 of the yellow flowers that I'd discovered; 20 of these were located in the north east quadrant of the site, the other 8 were widely scattered. I then randomly selected 20 purple-petaled flowers growing in the same area as the yellow ones. For each flower, I counted the number of anthers and the number of bracts along its peduncle, and I measured the height of the peduncle: from its base at the center of the rosette of pitcher leaves to the point of attachment of the sepals.

Literature search for annotated bibliography

My method of conducting the literature search, in hopes of seeking out all major references to *Darlingtonia* included searching two primary sources. I began by searching Biological Abstracts (published by Biosis, Philadelphia, PA) through March, 1997. References found there led me to additional works listed in their literature cited and bibliography sections. In addition I contacted state, federal and non-profit agencies whose

missions included rare plant study and protection in order to obtain any in-house publications. These sources included the U.S. Forest Service, the Fish and Wildlife Service, The Nature Conservancy, The California Native Plant Society, The California State Department of Fish and Game, The California Academy of Sciences, The International Carnivorous Plant Society and The Oregon Natural Heritage Program. Lastly, I searched for unpublished dissertations and master's theses through University Microfilms, Inc.

RESULTS

Results of seed set experiments

Data analysis was conducted using Microsoft Excel (version 5). Not surprisingly, the highest mean seed set was observed in the hand-pollinated blossoms, which received pollen from both natural and experimental sources (Table 1 and Figure 1). T-tests were used to determine if significant differences existed in seed set between certain pairs of treatments (Table 2). Seed set of the control (open-pollinated) treatment was 34% lower and significantly different ($p=0.0024$) from that of the hand-pollinated treatment (Table 2). As one might expect, the lowest mean seed set was observed in the pollinator-excluded treatment, which was significantly lower than the control seed set ($p=0.000$). Only 8 of the 30 flowers in the pollinator-excluded treatment matured fruit. The yellow-petaled flowers produced a 15% higher seed set over the controls yet were not sufficiently different to be statistically significant ($p=0.31$). Contrary to what one would expect, the seed set in the emasculated treatment was also slightly higher than in the controls (3%) yet again, not enough sufficiently so to be statistically significant ($p=0.88$). No seeds were set among the four surviving blossoms in the pollinator-excluded plus emasculated treatment, so this result was not included in the statistical analyses. Descriptive statistics of the five seed set experiments that produced fruit are summarized in Table 1 and illustrated graphically in Figure 2.

Table 1. Number of seeds set per fruit capsule in each of five treatments.

Treatment (N)	Mean±SE	Range	SD
Control (N=11)	1162±144	221-1616	480
Yellow-petaled (N=12)	1374±144	200-2007	498
Hand-pollinated (N=16)	1754±62	1275-2147	249
Emasculated (N=11)	1194±159	295-1855	526
Pollinator-excluded (N=8)	79±31	11-268	87

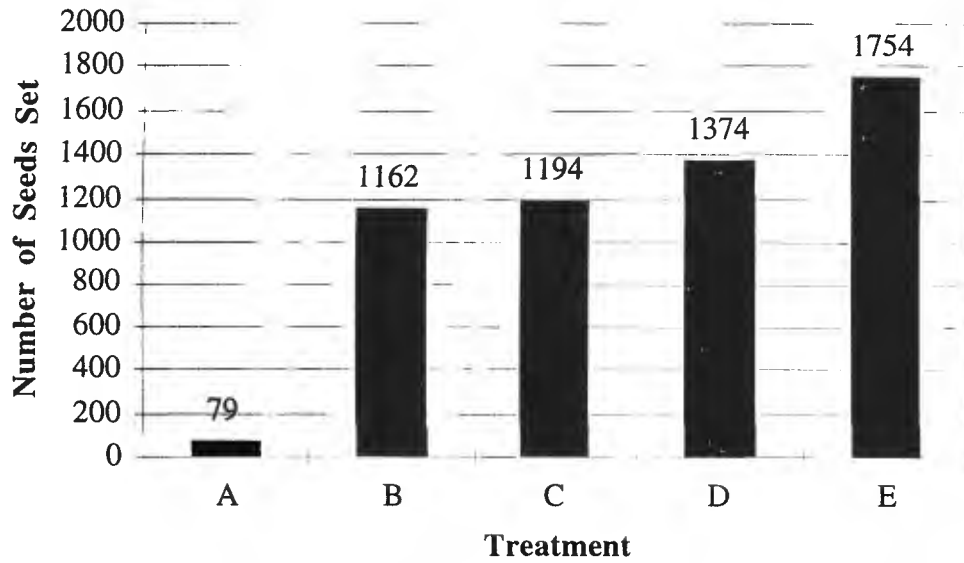


Figure 2. Average seed set for the five seed set treatments producing fruit. A= Pollinator-excluded, B= Control, C= Emasculated, D= Yellow-petaled, E= Hand-pollinated

Table 2. Results of t-tests (two-tailed, unequal variances) at 95% confidence level for seed set experiments.

Treatment Pair	T	P
Control vs. Emasculated	-0.15	0.88
Control vs. Hand-pollinated	3.76	0.0024
Control vs. Pollinator-excluded	-7.86	0.0000
Control vs. Yellow-petaled	1.04	0.31

Specimen survival

Some of the blossoms in each experiment withered and died within several days of being manipulated, possibly because the labels or bags were tied too tightly. Other blossoms disappeared, presumably having been trampled or eaten by animals. With the exception of the pollinator-excluded treatment, no flowers died later during the course of the experiment. Of the 30 flowers in the pollinator excluded treatment, 14 died during the course of the experiment, 8 survived but matured no seeds, and 8 matured some seeds. It is not clear whether the 22 flowers in the pollinator- excluded treatment died as a natural consequence of not being pollinated or if their deaths were due to handling damage.

Given the clear statistical results, the sample sizes were sufficiently large. Table 3 shows the number and percent of blossoms remaining to be censused at the end of the experiment.

Table 3. Survival of blossoms.

Treatment	# Blossoms Remaining	# of Original Blossoms	% Surviving
Control	11	20	55
Yellow-Petaled	12	20	60
Hand Pollinated	16	17	94
Emasculated	11	20	55
Pollinator-Excluded	30	30	100
Emasculated + Pollinator Excluded	4	20	20

Results of pollinator observations

Only once during this entire study (at the very beginning of my first field season) was a possible pollinator observed. One andrenid bee was seen at 1:00 P.M. on May 30, 1992. It behaved in a characteristic way. The bee landed on a *Darlingtonia* blossom and headed straight into one of the five entrance holes formed by the infolding of abutting petal edges. These holes appear to be the only location to enter the flower for any creature much larger than an aphid, and the andrenid bee was direct and purposeful in its entrance. I could observe the bee inside the flower through the relatively translucent petals as it seemingly foraged for pollen, which it did for approximately 5–10 seconds. It then exited through the same opening at which time I immediately collected it. Some pollen from the blossom's anthers was found on the bee's body.

The only other insects ever observed to land on a *Darlingtonia* blossom included some beetles, wasps and a bumblebee, but none proceeded to enter the blossom as the andrenid bee had, so none was collected.

No insects were caught in the flowers treated with Tanglefoot™ applications.

Comparative morphology of previously unreported yellow-petaled flower with typical purple-petaled variety.

Data analysis was conducted using Microsoft Excel (version 5). I found a total of 28 yellow-petaled flowers at the Grouse Ridge site. They were concentrated at the northeast corner of the site, yet some were found scattered across the rest of the site. Except for the yellow petals, it would have been hard to distinguish them from the typical purple-petaled flowers, for they did not seem to differ in any other readily observable way. Mean heights of yellow-petaled and purple-petaled flowers were 15.5 and 15.8 inches respectively, mean

number of anthers was 17.8 and 17.5 respectively, mean number of bracts was 9.5 and 9.3 respectively (Table 4.) .

In all three characteristics measured, height, number of anthers, and number of bracts, t-tests failed to reject the null hypothesis, as shown by the large 'p' values and critical values (Table 5.). Thus, there is insufficient evidence to conclude that the two varieties of flowers differ with respect to these characteristics.

Table 4. Morphological characteristics of yellow-petaled and purple-petaled blossoms at Grouse Ridge.

Flower	Height (in.)	# Anthers	# Bracts
Color	($X \pm SE$, SD, N)	($X \pm SE$, SD, N)	($X \pm SE$, SD, N)
Purple Petaled	15.8 \pm 0.9, 4.0, (20)	17.5 \pm 0.3, 1.2, (20)	9.3 \pm 0.3, 1.2, (20)
Yellow Petaled	15.5 \pm 0.5, 2.8, (28)	17.8 \pm 0.1, 0.8, (28)	9.5 \pm 0.2, 1.0, (28)

Table 5. Results of t-tests (two-tailed, unequal variances) at 95% confidence level comparing characteristics of yellow-petaled and purple-petaled flowers.

Character	'T' value	Critical value	'P' value
Height	-0.23	2.04	0.82
# Anthers	0.94	2.04	0.36
# Bracts	0.51	2.03	0.61

Literature search

As a result of the literature search, I found a total of 60 published accounts on *Darlingtonia* (Appendix III). These accounts were published in 35 different years and were spread over a 143 year period from 1853 to 1996. A majority of the literature is in scientific journals, but there are also book chapters, status reports, and theses. Subjects discussed included morphology, carnivory, insect associates and prey, habitat, status and threats, distribution, cultivation, and evolution. A majority of the publications focused on the species' morphology and its relationship to the carnivorous habit and the method of prey capture and digestion.

DISCUSSION

Discussion of seed set experiments

The results reported above provide clear evidence for the following conclusions:

1. Sexual reproduction occurred primarily through between-flower pollination.
2. Seed set was limited by competition for pollinator visitation.
3. Pollinators did not discriminate against yellow-petaled flowers.

1. Sexual reproduction occurred primarily through between-flower pollination. The significant difference between the mean seed set of control blossoms and pollinator-excluded blossoms shows that few seeds are set in the absence of pollinators as evidenced by the pollinator-excluded blossoms, where only eight out of 30 set any seeds at all. The few seeds that matured were probably a result of self-fertilization, since the bags were proven effective at excluding pollinators as was shown by the lack of seed set in the emasculated + pollinator-excluded blossoms.

The small seed set of the pollinator-excluded blossoms indicates that the species is at least marginally self-compatible (facultatively autogamous), but that it relies primarily on cross-pollination by some insect vector for a majority of its seed set. It is probable that several isolating mechanisms to reduce selfing are at work here, including spatial separation of anthers and stigmas and temporal separation of anther dehiscence and stigma receptivity. It is likely that the species is protandrous, with anther dehiscence occurring prior to stigma receptivity; this limits the occurrence of selfing. Although I did not conduct experiments to verify protandry, Dafni (1992) noted that protandry is more common and widespread throughout the angiosperms than protogyny. In addition, I observed that anther dehiscence begins simultaneously with flower anthesis, indirectly suggesting protandry since stigma receptivity occurring before the flower opens would not make reproductive sense.

It is possible that *Darlingtonia* exhibits sporophytic self-incompatibility, based on studies of the receptive surface of angiosperm stigmas (Heslop-Harrison and Shivanna 1977). Heslop-Harrison found that *Sarracenia* sp. (and many genera of the family's closest relatives) exhibited dry, papillate stigmas indicative of this breeding system.

Although I found a low occurrence of autogamy (as evidenced by the low pollinator-excluded seed set), geitonogamy (between-flower selfing) may be a common occurrence. Depending upon the average between-flower flight distance of pollinators, a significant percentage of a flower's seeds could be a result of pollination from other flowers of the same plant. This is due to the species' vigorous vegetative reproduction via rhizomatous growth which increases the likelihood that most of a flower's closest neighbors, from which it could receive pollen, would be from the same genetic individual. Thus, although autogamy is probably kept to a minimum by the spatial and temporal separation of male and female function, the rate of geitonogamy may be high if post-zygotic isolating mechanisms are absent. Unfortunately, the current study was designed to test only for natural levels of autogamy. *Darlingtonia*'s habit of growing in tight clumps makes determination of distinct genetic individuals nearly impossible.

It is not surprising that *Darlingtonia* sets some seeds in the absence of pollinators. Richards (1986) notes that facultative self-fertilization is widespread in the angiosperms and may have unexpected benefits including: guaranteed seed set in a pollinator's absence and in isolated plants, better use of pollen (lower pollen/ovule ratios), no stigma blockage by self-pollen, and fixation of highly adapted genotypes. Guaranteed seed set in isolated plants may be quite an adaptive advantage since *Darlingtonia*'s habitat is extremely disjunct. *Darlingtonia* seeps are generally small, and often separated by many miles.

The blossoms in the pollinator-excluded treatment lasted several days longer than the un-manipulated control blossom (that is they did not begin to senesce as soon). Schemske et

al. (1978) had similar findings. Perhaps flowers are genetically programmed to last longer if they haven't been pollinated yet, to increase their chances of setting seed.

A second line of evidence showing that sexual reproduction occurred primarily through between-flower pollination was the high seed set exhibited by the emasculated treatment, statistically similar to that of the control group. Results of the t-test ($t=-0.15$, $p=0.88$, 95 % confidence) support this conclusion. Thus, most of the pollen that contributes to fertilizing a flower's ovules comes from other flowers.

Dafni (1992) developed a simple index to measure self-incompatibility: divide the number of seeds set from self-pollination by the number of seeds set from cross pollination. Using my results, *Darlingtonia* would fall within Dafni's category of "mostly self-incompatible".

The observation of a high seed set in emasculated blossoms indicates that pollinator visitation was similar to that of un-manipulated control blossoms. This suggests that the pollinators either weren't able to perceive the fact that the blossoms lacked pollen, or that they were visiting the blossoms for rewards other than pollen. The second possibility suggests that pollen is not the main reward and that there may indeed be another reward such as nectar, although previous studies have failed to confirm the existence of nectaries (Debuhr 1973).

2. Seed set was limited by competition for pollinator visitation. The highly significant difference between the mean seed set of control blossoms and of hand-pollinated blossoms indicates that fruits were capable of maturing more ovules, given more frequent or effective pollinator visitation. I concluded, therefore, that reproductive potential was limited by competition for pollinators and not by competition for resources like sunlight, water, nutrients or space.

Since this study was unsuccessful in discovering a specific pollinator, it isn't clear whether the limitation is attributable to competition with sympatric species for a limited number of pollinators, low efficiency of pollinator visitation, or a shortage of pollinators resulting from unknown environmental effects in 1993. My failure to observe any pollinators despite extended observations, nor to capture any with the Tanglefoot™ applications suggests that indeed pollinators were few in number.

Results of the hand-pollination experiment suggest a means to estimate the maximum number of seeds which can be set, given unlimited pollen, and thus the maximum number of ovules that could be produced by a fruit capsule. Debuhr (1973) found that *Darlingtonia* produces from 1,750-2,000 ovules per ovary. My findings in the hand-pollination treatment of a mean seed set of 1,754 and a maximum seed set of 2,147, are within the same range and show that the species is capable of maturing all the ovules it produces, in the presence of an unlimited supply of pollen.

Assuming that the average number of seeds matured in the hand-pollination experiments is representative of the average number of ovules produced by a fruit, then an estimate of the percent of a fruit's ovules that it matures can be found by dividing the mean control seed set by the mean hand-pollinated seed set. Using this calculation, the average blossom matures just 66% of its total number of ovules. There may be little ecological significance to the finding that *Darlingtonia* does not set the maximum number of seeds that it is capable of setting. A less than maximum seed set does not necessarily mean that the species is at a reproductive disadvantage. On the contrary, the relatively high number of seeds produced is amazing considering that the primary mode of reproduction appears to be asexual reproduction by rhizomatous growth. Perhaps the species sets such a large number of seeds because of low viability, or to offset the fact that the probability of landing on a suitable substrate is low, given the species' strict habitat requirements.

3. Pollinators did not discriminate against the yellow-petaled blossom variety. No significant difference existed between the mean seed sets of control blossoms and that of yellow-petaled blossoms. Interestingly, though, the yellow-petaled blossoms set an average of 212 more seeds than the controls, a 15% higher seed set. One might assume such a rare blossoms color would either clearly be favored by, or discriminated against by pollinators. Since this study is the first to describe this color variety, there are no other studies with which to compare my results. However, previous studies involving other plant species have found strong evidence of pollinator discrimination against rare color varieties (Kearns and Inouye 1993). One possible reason that discrimination did not take place is that morphology and phenology of yellow and typical blossoms were found to be statistically similar.

The conclusion that pollinators do not discriminate against yellow-petaled blossoms is based on the assumption that the observed seed set was a result of pollinator visitation, not of self-pollination. I reasoned that the level of autogamy in yellow-petaled blossoms would be similarly low to that observed in typical blossoms, as shown by the results of the pollinator-exclusion treatments. Thus, I chose not to conduct pollinator-exclusion and emasculation treatments on the yellow-petaled blossoms especially since the total number of yellow-petaled blossoms was so small.

If pollinators do indeed visit both flower colors with equal frequency, then the abundance of yellow flowers may increase over time. The fact that this variety has been observed only at Grouse Ridge, possibly the southern-most *Darlingtonia* seep, suggests it arose there because the genetics of that population were most divergent.

Pollinator observations

The observation of the andrenid bee early in the study led me to believe that pollinator observations would be more successful than they were. Since the bee was observed during the afternoon, when the *Darlingtonia* blossoms were in full bloom, I concentrated my subsequent observations at that time, without luck. In fact, few andrenids were seen in the course of my studies.

Although insects were quite numerous at both sites, as would be expected in such a warm and wet environment, and many appeared to be visiting flowers of other species, they seemed to actively avoid landing on or inspecting the *Darlingtonia* blossoms. One would think that the copious amount of pollen produced by the species would attract a wide variety of insects.

Evidence for a biotic pollinator seems strong, and comes from two sources: The low seed set in pollinator-excluded blossoms, and the high seed set of emasculated blossoms. Wind pollination would be the only other alternative, but highly unlikely considering the flower's morphology.

Although this study failed to discover the identity of any pollinators, besides the incidental observation of the Andrenid bee, the results have ruled out routine selfing as a reason for the lack of pollinator observations. Juniper (1989) noted that “few workers have made even the briefest of comments on the pollination of carnivorous plants, although it is generally considered, with incomplete evidence, that all carnivorous plants are insect pollinated.” A pollinator, therefore must exist; its identity simply has not been discovered.

An argument for a single (oligophily) or few species of pollinators could be made on the basis of the precise behavior required to find the entrance to the blossom through the narrow openings. Dafni (1992) notes that presence of flowers requiring such precise behaviors may suggest there is a single pollinator for that species because the ‘handling

cost' would be too high if the pollinator were not specialized for it. Optimal foraging theory would suggest that the complexity of learning to handle such a flower would make specialization on that flower necessary to make the cost-benefit ratio favorable. Why would a pollinator bother with such a complex flower? The reward would be high in terms of the amount of pollen produced, and the closed corolla ensures that few illegitimate visitors will be robbing pollen without performing pollination. Thus, even if the flower were hard to handle, the benefit of copious amounts of pollen and few competitors should make it a rewarding choice. In addition, the fact that *Darlingtonia* is among the earliest spring bloomers would give organisms who learned to handle it a significant advantage since it may be one of the only pollen sources around for newly emerged bees, etc. The flower complexity suggests the highly evolved bees as possible pollinators. *Darlingtonia*'s closest relatives, *Sarracenia*, are pollinated by various 'bumblebees' (Folkerts 1982).

In summary, no longer can a failure to observe a pollinator be attributable to a breeding system of routine self-pollination.

Comparative morphology of yellow-petaled flower with typical purple-petaled variety

To my knowledge, based on an extensive literature search, no previously published account exists of a yellow-petaled flower variety of *Darlingtonia californica*. In addition, it is uncertain whether this variety occurs anywhere other than where I observed it at the Grouse Ridge study site, in Nevada County, California. J. Hawkeye Rondeau, author of 'Carnivorous Plants of the West' (Rondeau 1995), has visited over 130 *Darlingtonia* sites throughout California and Oregon, and reports that he has never seen this variety in any other location (pers. comm).

Little variability in measured characters existed within the two groups as evidenced by their small standard deviations. This finding is consistent with the literature. For example,

Debuhr (1973) observed that flower height was relatively uniform in any one population at any one time, but did vary between sites and years.

The morphological similarities observed between purple-petaled and yellow-petaled flowers may be a reason that pollinator discrimination was not observed in the seed set experiments. Of course, there may be additional similarities in characters such as scent, nectar and ultra-violet guides, that may be more significant in influencing pollinator behavior. Although I made no statistical comparisons, informal observations suggested that the two varieties were also similar in blooming season and rate of flower maturation.

The average number of anthers in the typical purple-petaled flower was found to be slightly higher in this study (17.8 anthers) than that which has been reported in the literature (15 anthers) by Debuhr (1973). Since this study is the first to report the existence of a yellow-petaled variety, there is no previous literature with which to compare its measured characteristics.

Discussion of literature search

The literature search revealed that numerous investigators have studied the nature of *Darlingtonia*'s carnivorous habit. It is also clear, however, that there has been a notable absence of quantitative field investigations into the species' habitat, ecological relationships, and especially reproductive and pollination biology. This should be good news to graduate students searching for meaningful topics of study, for here the field is wide-open, with many intriguing questions yet to be answered!

Summary of major findings

The most notable result of this study was the two forms of evidence suggesting that *Darlingtonia* does not rely on self-pollination and that consequently a biotic pollinator must exist, despite its lack of detection. The discovery of a yellow-petaled flower variety that exists in a single known location was unexpected, along with the observation that pollinators failed to discriminate against the rare color.

Like most studies, this project has raised more questions than it has answered. The identity of *Darlingtonia*'s pollinator has become an even more intriguing mystery due to its elusiveness in this study.

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APPENDIX I

FLORISTIC SURVEY OF GROUSE RIDGE STUDY SITE

Identified by Christine Elder using Hickman (1993)

Trees

Pinus contorta, *Alnus tenuifolia*, *Calocedrus decurrens*

Shrubs

Vaccinium sp.

Herbs

Darlingtonia californica, *Polygonum bistortoides*, *Saxifraga oregana*, *Drosera rotundifolia*, *Orobanche uniflora*, *Platanthera sparsiflora*, *Platanthera leucostachys*, *Mimulus guttatus*, *Mimulus moschatus*, *Viola glabella*, *Viola macloskeyi*, *Actaea rubra*, *Mitella breweri*, *Hastingsia alba*, *Veratrum californicum*, *Listera convallarioides*, *Pedicularis attollens*, *Galium trifidum*, *Epilobium oregonense*, *Epilobium ciliatum*, *Circaea alpina*, *Senecio triangularis*, *Dodecatheon sp.*, *Ranunculus sp.*

Graminoids

Cyperus sp., *Carex sp.*, *Eleocharis sp.*

APPENDIX II

FLORISTIC SURVEY OF MOUNT EDDY STUDY SITE

Identified by Christine Elder using Hickman (1993) and Whipple (1981)

Trees

Pinus monticola, *Pinus contorta*, *Abies magnifica*

Shrubs

Artemisia tridentata, *Spirea sp.*, *Alnus sp.*

Herbs

Lilium maritimum, *Hastingsia alba*, *Tofieldia occidentalis ssp. occidentalis*, *Narthecium californicum*, *Aconitum columbianum*, *Platanthera leucostachys* and *P. sparsiflora*, *Aquilegia formosa*, *Veratrum californicum*, *Calochortus persistens*, *Dodecatheon sp.*, *Heracleum lanatum*, *Perideridia sp.*, *Oenanthe sp.*, *Polygonum bistortoides*, *Aster alpigenus var. andersonii*, *Caltha leptosepala var. biflora*, *Achillea millefolium*, *Epilobium ciliatum ssp. ciliatum*, *Sidalcea sp.*, *Sisyrinchium sp.*, *Smilacina sp.*, *Mimulus guttatus*, *Delphinium sp.*, *Senecio triangularis*, *Potentilla sp.*, *Taraxacum officinale*, *Allium sp.*, *Orthocarpus sp.*, *Phacelia sp.*, *Trifolium sp.*

APPENDIX III-ANNOTATED BIBLIOGRAPHY

This annotated bibliography is the first of its kind and includes all known articles, papers, books, unpublished reports, and master's theses focusing on any aspect of the biology of *Darlingtonia californica*. Also included are general books on carnivorous plants that have in-depth chapters dedicated to the species. It was compiled by searching the literature and searching Biological Abstracts (published by Biosis, Philadelphia PA) through July, 1995.

Adams, R.M. and G.W. Smith. 1977. An S.E.M. survey of the five carnivorous pitcher plant genera. *American Journal of Botany* 64(3): 265-272.

Adams used S.E.M. (scanning electron microscopy) to observe pitcher morphology related to prey attraction, capture and digestion in five genera belonging to three distantly related families. S.E.M. photographs of *Darlingtonia* included the upward-pointing hairs, nectar glands and stomates of the fishtail appendage, the downward-pointing hairs lining the pitcher interior and a vertical section of the entire pitcher leaf. No digestive glands were observed, supporting the belief that *Darlingtonia* relies not on enzymes, but on symbionts to accomplish prey digestion. Adams concludes that "due to the differences in the phylogenetic origins of these five genera, the obvious similarity in pitcher morphology must be due to convergent evolution."

Arber, A. 1941. On the morphology of the pitcher-leaves in *Heliophora*, *Sarracenia*, *Darlingtonia*, *Cephalotus*, and *Nepenthes*. *Annals of Botany* 5: 563-578.

Arber compares and interprets the morphology of the five pitcher-leaf bearing genera of carnivorous plants. Includes two pages describing the leaf of *Darlingtonia* along with a drawing illustrating its pattern of venation.

Austin, R. M. 1875-1877. Letters to W. M. Canby on *Darlingtonia*. The Society of Natural History of Delaware, Wilmington, DE: Wilmington Institute Free Library.

These are the letters and manuscript journal of amateur botanist Rebecca Austin, corresponding with the esteemed American botanist, William Canby. Mrs. Austin was the first to observe the species at length in the field, and her observations are thorough and insightful.

Bell, C.R. 1949. A cytotaxonomic study of the Sarraceniaceae of North America. *Journal of the Mitchell Society* 65:137-166.

Bell made anther smears and root tip smears to observe the chromosomes of *Sarracenia* ssp. and *Darlingtonia* (which in this paper is referred to by its old name *Chrysamphora californica*). Bell found *Darlingtonia* to possess an unreduced number of 30 chromosomes, which averaged 1.5 microns in length. Four were slightly longer than the other 26, two of which usually had a pair of large satellites. Chromosome number and size differed from that found in the species of *Sarracenia*, and Bell notes that this difference gives further proof of the taxonomic and morphological individuality of the two genera.

Brownfield, J. 1985. Rearing cobras. *Carnivorous Plant Newsletter* 14: 78-80.

Brownfield offers her suggestions on cultivation. She found that *Darlingtonia* thrives best when provided with 14 hours of light, high humidity and cool, fresh water bathing its roots.

California Department of Fish and Game. 1995. Natural diversity data base. Rare-find database for the 'Darlingtonia seep' community type as of 1/6/95.

Includes status reports, ecological notes and partial floras for a majority of the known sites supporting the species in California.

Canby, W.M. 1874. *Darlingtonia californica*, an insectivorous plant. Proceedings of the American Association for the Advancement of Science. 1874: 64-72.

Canby's article is the first to provide a detailed description of the species' morphology as it relates to carnivory, although it was based solely on examination of dried specimens and the field observations of Canby's acquaintance, J.G. Lemmon, in northern California. Canby makes comparisons with the more well-known *Sarracenia* sp.

Cheatham, N. 1976. Butterfly Valley Botanical Area. *Fremontia* 4: 3-8.

Cheatham describes the famous vegetation, early inhabitants and history of Butterfly Valley, a Forest Service Botanical Area near Quincy, California that was created to protect its rich and diverse flora including *Darlingtonia*. Cheatham also provides a biographical sketch of Rebecca Austin, the amateur naturalist who was the first to study *Darlingtonia* in its natural habitat. She lived in Butterfly Valley in the late 1800's and corresponded extensively with eminent American botanist William Canby, detailing her observations and experiments on the species.

Clark, R.D. 1990. What's in a name? *Darlingtonia californica*. *Oregon Coast* March/April: 8-19.

Clark describes his journey in search of the exact locale where the species was first discovered. Its discoverers were the men of the United States Exploring Expedition of 1838-1842, including eminent geologist James Dana and Titian Peale, son of the American portrait painter Charles Willson Peale. They collected the specimens John

Torrey would eventually use in preparing the first official botanical description. Clark includes excerpts from the men's detailed journals, which enabled him to pinpoint the discovery site, located near Castle Crags State Park in northern California. Clark also provides a short account on the naming of the species.

Debuhr, L. E. 1973. Distribution and reproductive biology of *Darlingtonia californica*.

Unpublished master's thesis, Claremont Graduate School, Claremont, California. 42 pp.

Debuhr made tissue slides of reproductive structures, including the peduncle, bud, perianth, stamens, pollen, ovary, fruit and seeds. He noted aspects of the floral structure that aid in pollination, such as contrasting colors, nectar glands, and directional papillae. Debuhr also determined the extent of the species' range and its habitat parameters by inspecting herbarium specimens and herbarium label information. A complete list of the herbarium specimen collection sites in California and Oregon is included as well as a map of the species' distribution.

Debuhr, L.E. 1974. The distribution of *Darlingtonia californica*. Carnivorous Plant Newsletter 3: 24-26.

Debuhr summarizes the distribution of the species, includes a map and notes some of the ecological parameters that dictate its distribution.

Debuhr, L.E. 1975. Phylogenetic relationships of the Sarraceniaceae. Taxon 24 (2/3): 297-306.

Debuhr argues for placing the Sarraceniaceae in a suborder in the Theales, based on the numerous shared floral and vegetative characters, and discusses their significance. He reviews the work of previous researchers into the phylogenetic relationships of carnivorous plant families, and concludes they are only distantly related to each other, including the Sarraceniaceae. Their similarities are attributed to convergent evolution.

Debuhr, L.E. 1977. Wood anatomy of the Sarraceniaceae; ecological and evolutionary implications. *Plant Systematics and Evolution* 128:159-169.

Debuhr provides quantitative descriptions and comparisons of wood anatomy, including tracheids, vessel elements and parenchyma of the genera *Darlingtonia*, *Heliophora* ssp. and *Sarracenia* spp. He believes that "features of the wood may offer more information on the phyletic relationships of the family than features of the leaves" due to their extreme modifications for carnivory. Some characters of the wood of *Darlingtonia* and *Sarracenia* spp. exhibit evolutionary specializations and advancements over that of *Heliophora* spp. Debuhr suggests various implications of these differences.

Dwyer, T. P. 1983. Seed structure of carnivorous plants. *Carnivorous Plant Newsletter* 12: 8-23.

Dwyer provides anatomical descriptions and an identification key to the seeds of many carnivorous plant species. High-quality illustrations and SEM photographs of many, including *Darlingtonia*, are included, as well as a glossary of terms used to describe seed structure.

Edwards, H. 1876. *Darlingtonia californica*. Text of a talk given to the California Academy of Sciences. *Proceedings of the California Academy of Sciences* 6: 161-166.

Edwards provides an early account of the discovery, natural history and pitcher morphology of the species. He also discusses the results of his analysis of 43 pitcher leaves in which he identified 43 taxa of prey, including beetles, bees, grasshoppers, flies, butterflies, spiders and bugs. He also discovered some non-prey associates including spiders, flies and moths.

Elder, C. 1993. *Darlingtonia* midge. ECONIEWS, newsletter of the Northcoast Environmental Center, Arcata, California 23 (6): 11.

Elder describes the natural history and ecology of the pitcher-leaf inhabiting midge fly, *Metriocnemus edwardsi*. The midge is thought to be an obligate associate of the species. It lays its eggs within the leaf, where the larvae live and feed on decomposing prey captured by the plant. The relationship is mutualistic, for the larvae mechanically break down the prey's exoskeletons, enabling the leaf to more easily absorb the nutrients.

Elder, C. 1994. Reproductive biology of the California pitcher plant, *Darlingtonia californica*. *Fremontia* 22 (3): 29-30.

Lack of pollinator observations by previous investigators before her led the author to investigate whether this was attributable to an absence of pollinators due to routine selfing. She found few to no seeds were set by flowers deprived of pollinator visitation, while flowers with anthers removed set as many seeds as unmanipulated flowers. These experiments indicate that *Darlingtonia* relies primarily on cross-pollination to effect seed set. Unmanipulated flowers set high numbers of seeds, but not as many as those in which extra pollen had been experimentally added, suggesting that seed set is limited more by competition for pollination than for other resources. Elder conducted the first systematic search for the pollinating agent, but like others before her, failed to discover a likely pollinator, although several beetles and members of the hymenoptera were possible candidates. She also studied aspects of the plant's ecology, including density, dispersion pattern, floral morphology and flowering phenology.

Fowlie, J. A. 1982. Notes of the habitat and ecological relationships of *Cypripedium californicum* A. Gray and *Darlingtonia californica*. Orchid Digest Sept.-Oct. :165-170.

Fowlie describes the habitat characteristics of a site in northern California where *Cypripedium* orchids and *Darlingtonia* are found growing together.

Franck, D. H. 1975. Early histogenesis of the adult leaves of *Darlingtonia californica* (Sarraceniaceae) and its bearing on the nature of epiascidiate foliar appendages.

American Journal of Botany 62 (2):116-132.

Franck described the morphological development of *Darlingtonia*'s shoot tips, leaf primordia and pitcher leaves. Its leaf is an example of an epiascidiate foliar appendage: a tubular organ whose evolutionary upper leaf surface forms the inside of the tube. Such leaves are ontogenetically complex, and are found throughout the Sarraceniaceae and select genera in other carnivorous plant families.

Franck, D.H. 1976. Comparative morphology and early leaf histogenesis of adult and juvenile leaves of *Darlingtonia californica* and their bearing on the concept of heterophylly. Botanical Gazette 137 (1): 20-34.

Franck described and compared in detail the morphology and early development of juvenile and adult pitcher leaves. Juvenile leaves differ from adult leaves in their lack of both a keel and fishtail appendage, as well as their smaller size and simpler venation patterns. Franck demonstrates that juvenile leaves are not simply morphologically arrested forms of adult leaves, but that they differ ontogenetically at even the earliest stages of development.

Glossner, F. 1992. Ultraviolet patterns in the traps and flowers of some carnivorous plants Bot. Jahrb. Syst. 113: 577-587.

Glossner found distinct ultraviolet patterns caused by the absorption and reflection of UV light on the pitcher leaves of *Darlingtonia* and other species of carnivorous plants.

Green areas of the pitcher leaf were UV-absorbing; the fenestrations of the pitcher were UV-reflecting. He suggests these UV patterns serve as visual cues in the attraction of insect prey. He found that the flowers and traps of other species of carnivorous plants differed in size, shape and contrast of UV patterns, and theorized that this may assist pollinating insects in differentiating between flowers and traps, thus avoiding becoming prey.

Gray, A. 1853. On *Darlingtonia californica*, a new pitcher-plant from northern California; by John Torrey, F.L.S. American Journal of Science and Arts Second series 16: 425.

Gray published a short excerpt of Torrey's original monograph on the species by the same title.

Gray, A. 1863. Comments on *Darlingtonia californica*. American Journal of Science and Arts Series B 35: 136-137.

Gray offers the first description of the seed of *Darlingtonia*, obtained near Mount Shasta, California, from William H. Brewer of the California Geological Survey.

Hepburn, J. S. , F. M. Jones and E. Q. St. John. 1927. Biochemical studies of the North American Sarraceniaceae. Transactions of Wagner Free Institute of Science of Philadelphia 11: 1-91.

Hepburn et al studied the biochemical nature of the fluid produced by the pitcher leaves, and they give a thorough account of the findings of previous investigators. They were the first to show that the plants undoubtedly use their prey as a source of minerals.

Their studies focused on the more well-known and readily available *Sarracenia*s although some work was done on *Darlingtonia*. They found that the insect-attracting nectar on the outer surface of the pitcher leaves of *Darlingtonia* is composed of fructose. They measured the volume of pitcher secretions, which they also found to be neutral in acidity. The authors added various organic substances to the leaves and

found that this stimulated the leaf to secrete additional liquid. They determined that the liquid had no stupifying qualities, and merely acted to drown the captured insects. In addition, digestive enzymes, such as protease were found in some *Sarracenia*'s, but not in the pitcher liquid of *Darlingtonia*. The pitcher liquid was found to be sterile in immature, unopened leaves, and to contain numerous kinds of bacteria in mature, open leaves. The authors determined that the presence of proteolytic bacteria must play an important role in prey digestion in *Darlingtonia*, since it lacks digestive enzymes. They found that nitrogen and phosphates are absorbed by the leaf. Studies were also made of the chemical composition of the plant tissues.

Heslop-Harrison, Y. 1978. Carnivorous plants. *Scientific American* 78: 104-115.

An excellent overview of carnivorous plants, especially their structures related to their carnivorous habit. Provides a list of genera of carnivorous plants and the digestive enzymes in each; and shows that *Darlingtonia* may have protease and possibly amylase and invertase. The author notes that the principle benefit of the carnivorous habit may be in obtaining additional phosphorus, not nitrogen as has been widely assumed.

Hooker, J. 1871. *Darlingtonia californica*, Native of California. *Curtis's Botanical Magazine* 27 (3): Tab 5920.

Hooker, a British botanist associated with the Royal Gardens, presents excerpts from a letter he received from W. Robinson, who, in 1870, visited the species in its native habitat. Notes include habit and habitat.

Hooker, J. 1875. Address to the Department of Botany and Zoology. Report of the 44th meeting of the British Association for the Advancement of Science. Belfast. 1874:110-111.

Hooker was the first to note that *Darlingtonia* produces a morphologically distinct juvenile leaf, and that it resembles the adult leaf of some *Sarracenia*. He comments on the possible evolutionary significance of this similarity.

Hornback, R. 1987. The Cobra Lily. *Pacific Horticulture*. Summer: 48-52.

This is among the best of the general-interest articles written thus far on *Darlingtonia*. It colorfully describes the species, its distribution, habitat, botanical history, and carnivorous nature. Written with the horticulturalist in mind, it briefly describes the difficulties in propagating the species and lists several sources for obtaining seeds and live plants.

Horner, S. 1976. Unpublished report on the status of *Darlingtonia californica* on the Mt. Shasta district, Shasta-Trinity National Forest, U.S. Forest Service. 3 pp.

Horner gives a short description of the species, its habit and habitat and known and potential threats to populations occurring on the district.

Joel, D. M. 1988. Mimicry and mutualism in carnivorous pitcher plants (Sarraceniaceae, Nepenthaceae, Cephalotaceae, Bromeliaceae). *Biological Journal of the Linnean Society* 35: 185-197.

Some workers have suggested that the pitcher-leaves of these carnivorous species are Batesian mimics: they resemble their flowers in order to deceive insect visitors into becoming prey. In contrast, Joel argues against Batesian mimicry and suggests that it is more accurate to characterize the relationship between insect and plant as mutualistic. A majority of the insect visitors benefit by feeding on the pitcher's nectar and in return sacrifice only a small percent of their population as prey.

Juniper, B. E., Robins, R. J. and D. M. Joel. 1989. *The Carnivorous Plants*. Academic Press, Inc., San Diego, California. 353 pp.

This work has replaced Lloyd (1942) as the definitive guide to carnivorous plant biology. Of the many books on carnivorous plants, this is the most up-to-date and scientific and contains many citations for further reading. Unlike other books, its chapters are organized not by species but by topic, with chapters on taxonomy, evolution and morphological adaptations to carnivory among others.

Keeler-Wolf, T. 1982. An ecological survey of the proposed Cedar Basin research natural area, Shasta-Trinity National Forest, California. Unpublished report to the Forest Service (purchase order 40-9AD6-2-606), on file at the Pacific Southwest Forest and Range Experimental Center, Berkeley, CA 75 pp.

Keeler-Wolf provides an in-depth report on the geology, climate, fauna, flora and vegetation types of this proposed research natural area. The area, particularly around Cedar and Lower Cliff Lakes, supports stands of *Darlingtonia*.

Keeler-Wolf, T. 1986. An ecological survey of the proposed Stone Corral-Josephine Peridotite research natural area (L.E. Horton-Darlingtonia bog research natural area) on the Six Rivers National Forest, Del Norte County, California. Unpublished report to the Forest Service, purchase order 40-9AD6-5-907), on file at the Pacific Southwest Forest and Range Experimental Center, Berkeley, CA 69 pages.

Keeler-Wolf provides an in-depth report on the geology, climate, fauna, flora and vegetation types of this proposed research natural area. He notes that the species assemblage living sympatrically with *Darlingtonia* at this site differs from those at other candidate research natural areas.

Knight, W. and I. and J.T. Howell. 1970. A vegetational survey of the Butterfly Botanical Area. *The Wasmann Journal of Biology* 28: 1-46.

Knight provides a flora of Butterfly Valley, the species-rich area where *Darlingtonia* was first studied. Butterfly Valley supports the most species of carnivorous plants living sympatrically—including *Darlingtonia*, *Drosera*, and two genera of *Utricularia*.

Lloyd, F.E. 1942. *The carnivorous plants*. Chronica Botanica Co. Waltham, Mass. 352 pp.

Lloyd's book was the 'bible' of carnivorous plant tomes of his era. The chapter on *Darlingtonia* includes its discovery, distribution and habitat, with a lengthy description of its morphology, especially as it relates to its carnivorous habit.

Lutz, C. L. and E. Magi. 1980. A preliminary description of *Darlingtonia* bogs. U.S. Forest Service. 15 pp.

This unpublished report to the Forest Service describes various ecological parameters of *Darlingtonia* bogs. The workers visited sites throughout the species' range, collected information on soil and water chemistry, slope and exposure, and identified sympatric species. Using floristic and geographic similarities, they classify sites as belonging to one of three categories: coastal Oregon bogs, Siskiyou Mountain bogs and California interior bogs.

Macfarlane, J. M. 1889. Observations on pitcher insectivorous plants (part I). *Annals of Botany* 3: 254-266.

Macfarlane was the earliest researcher to utilize the microscope to examine the anatomy of *Darlingtonia's* leaf. He provides some brief notes on vascularization and anatomical similarities to other pitcher plant genera.

Macfarlane, J.M. 1889. Observations on pitched insectivorous plants (part II). *Annals of Botany* 7: 403-458.

In this second part of Macfarlane's work, he continues to study and compare the leaf histology of *Darlingtonia*, *Nepenthes*, *Heliamphora* and *Sarracenia*. He examines the structure of *Darlingtonia*'s cells and hairs over the inner and outer leaf surfaces, and he describes how their structure aids in prey attraction and capture.

Mellichamp, T.L. 1978. Botanical history of CP II: *Darlingtonia*. *Carnivorous Plant Newsletter* 7(3): 82-85.

Mellichamp recounts the colorful botanical history of *Darlingtonia*. He briefly describes the roles of three men who figured most prominently in the species history: William D. Brackenridge, botanist with the U.S. Exploring Expedition who discovered the species in 1841; John Torrey, who published the first official description and Dr. William Darlington, a respected botanist for whom Torrey named the species.

Mellichamp, T.L. 1983. Cobras of the Pacific Northwest. *Natural History* 4: 47-50.

Mellichamp provides a brief ecology and natural history of *Darlingtonia*, also known as the cobra lily, from which the article gets its name. His speculations on the evolutionary history of the species, the first ones published to date, suggest the Sarraceniaceae originated 70 million years ago during the late Cretaceous era in what is now the southeastern United States. *Darlingtonia*'s ancestors moved west across the subtropical plains, reaching the West Coast by 40 million years ago, because a progressively drier climate and the rise of the Rockies and Sierra Nevada would have prevented a later westward dispersal. Today, *Darlingtonia*, survives as a relictual species in the mountains of northwestern California. Like many of its neighbors, its closest relatives are found in the moist forests of the Southeast, giving further proof of the species' evolutionary beginnings.

Naeem, S. and J. Dushek. 1985. Plumbing the deathly depths of the California pitcher plant. *Pacific Discovery* 38 (2): 26-31.

Naeem presents an entertaining and informative summary of his research on pitcher inhabitants (see following article), conducted while attending the University of California at Berkeley. He found that the pitcher-leaf contains not only its prey, but that it supports a wide variety of aquatic organisms such as copepods, protozoans and bacteria that may play a role in prey digestion.

Naeem, S. 1988. Resource heterogeneity fosters coexistence of a mite and a midge in pitcher plants. *Ecological Monographs* 58 (3): 215-227.

Naeem studied two obligate inhabitants of *Darlingtonia's* pitcher, their means of coexisting and their beneficial role in aiding the plant's nutrient uptake from its prey. Competition theory suggests that species utilizing the same limited resource cannot coexist indefinitely. However, Naeem's experiments show that the mite and midge avoid direct competition due to differences in their feeding behavior and natural history. If resource levels were to be held constant, it is likely that the midge would eventually out-competed the mite since it is 36 times larger. However, resource levels vary considerably, allowing the mite with its faster life cycle to 'track' the resource better than the longer-lived midge.

Nielsen, D. W. 1990. Arthropod communities associated with *Darlingtonia californica*. *Annals of the Entomological Society of America* 83(2): 189-200.

Nielsen presents the results of his thesis research conducted at Humboldt State University, California. He collected pitchers from various sites in northwestern California and identified 21 species of arthropod associates, including four previously un-described species. He found the species compositions of the communities varied significantly between sites. Nielsen describes each species, its location and behavior

while on the pitcher, density, frequency of occurrence and host-parasite relationships when observed. A chironomid midge, *Metriocnemus edwardsi*, was the most abundant and frequent associate observed during the study.

Oregon Natural Heritage Program (ONHP) 1995. Oregon Rare and Endangered Plant Project. ONHP, Portland, Oregon

The ONHP collects information on species of concern, including *Darlingtonia*, which include site reports, element occurrence records, status reports, habitat information including associated species, and threats to conservation.

Pickart, A. and K. Berg. 1986. A portfolio of *Darlingtonia* bog wildflowers. *Fremontia* 14 (2): 13-17.

A beautifully illustrated portfolio showing wildflowers found sympatrically with *Darlingtonia*, including orchids (*Platanthera sparsifolia*, *P. dilatata* and *Cypripedium californicum*) and lilies (*L. wigginsii*, *Tofieldia glutinosa* and *Narthecium californica*).

Rondeau, H. 1995. Carnivorous plants of the west, volume II: California, Oregon, Washington. Self-published. 37 Sunnyslope, San Jose, CA. 95127. 60 pp.

Rondeau provides detailed descriptions of the West's carnivorous plant species, including *Darlingtonia californica*. He includes information on morphology, trap structure and function, prey and insect associates, habitat and associated species, as well as range maps and color photographs. Rondeau has traveled extensively in search of carnivorous plants in general and *Darlingtonia* in particular—he has visited over 100 *Darlingtonia* sites in California and over 30 sites in Oregon.

Sawyer, J. 1986. *Darlingtonia* seeps. *Fremontia* 14 (2): 18.

Sawyer suggests that *Darlingtonia*'s habitat be called 'seeps' in place of the often used terms 'bog', 'fen' or 'mire'. A 'seep' is perennially irrigated with fresh ground water from a spring or creek, while a bog is a European term for a peat land irrigated only

from rain and snow falling directly on it. Both seeps and bogs are similar in supporting carnivorous plants in a nutrient-poor habitat.

Sawyer, J. 1978. An ecological survey of the proposed Preacher Meadows research natural area, Trinity County, California. Unpublished report to Region 5/PSW Research Natural Area Committee, U.S. Forest Service.

Sawyer describes the topography, climate, geology and flora of the area and recommends it be designated a research natural area. He conducted a floristic survey of the area and identified 164 taxa, including a "striking abundance of *Darlingtonia*".

Sawyer, J. and T. Keeler-Wolf. 1996. A manual of California vegetation. California Native Plant Society Publication, Sacramento, CA. 412 pp.

Sawyer and Keeler-Wolf give a brief description of *Darlingtonia* and its habitat. They named the plant association where it is the dominant herb in the ground canopy the 'Darlingtonia series', and list ten common sympatric species.

Schnell, D. E. 1976. Carnivorous plants of the U.S. and Canada. John F. Blair Pub. U.S.A. 125 pages.

Schnell's four page chapter on *Darlingtonia* is a basic introduction to the species, its range, habitat, and morphology. A generalized range map and color photography of the plant are included.

Sheridan, P. and B. Scholl. 1993. Notes on some *Darlingtonia californica* Torr. Bogs. Carnivorous Plant Newsletter 22 (3): 70-75.

The authors describe six sites in the Siskiyou National Forest of northern California/southern Oregon visited during August, 1988. They give brief descriptions of the sites including lists of common sympatric species. Average air temperature was 22 c., while water temperature in the bogs was 13 c. Such cool water temperatures

were determined to be essential for successful cultivation of the species in the south-eastern U.S. where the authors conducted informal experiments.

Skinner, M.W. and B.M. Pavlik. (eds.). 1994. California Native Plant Society's inventory of rare and endangered vascular plants of California. Special publication No. 1. Fifth Edition. California Native Plant Society, Sac., CA. 338 pp.

Darlingtonia californica is considered by the CNPS as a 'list 4' species (a plant of limited distribution) with an R-E-D code of 1-2-1, (a plant found in sufficient numbers and distributed widely enough that its potential for extinction is currently low). It is considered endangered in part of its range, threatened by horticultural collecting and mining. It is a federal C3c species (too widespread and/or not sufficiently threatened to warrant listing), has no California status and is on the watch list in Oregon.

Slack, A. 1980. Carnivorous Plants. MIT Press, Cambridge, MASS. 240 pp.

Slack's book includes a three-page chapter on *Darlingtonia* very similar in scope and content to Schnell (1976). In the chapter on cultivation, Slack dedicates two pages to *Darlingtonia* in which he describes his successful growing techniques and methods of propagating the species, both from seeds and from cuttings.

Stansell, V. 1980. *Darlingtonia californica*. Geographical distribution, habitat, and threats. Unpublished report of the U.S. Fish and Wildlife Service, Endangered Species Office, Portland, Oregon. 19 pp.

Stansell's study was initiated in response to the FWS listing of the species as a candidate for Threatened status under the Endangered Species Act. She reviews its life history, habitat, geographical distribution (map included), threats and conservation efforts, and offers recommendations. The species is primarily threatened by consumer-driven horticultural collecting and by lack of success in commercial cultivation. Other threats include mining, road construction and housing projects. Her field sampling

yielded a list of species frequently associated with *Darlingtonia*, including rare orchids and violets.

Szerlip, S. 1975. Insect associates (Diptera: Chironomidae, Sphaeroceridae) of *Darlingtonia californica* (Sarraceniaceae) in California. *Pan-Pacific Entomologist*. 51(2):169-170.

Szerlip observed larvae of *Metriocnemus edwardsi* (a chironomid midge) and larvae and adults of *Leptocera* (a sphaerocerid) inhabiting *Darlingtonia* pitchers at a site in Nevada County, California. Of the 17 described species of *Metriocnemus* in North America, *M. edwardsi* is the only as yet found in the state. He notes that the *Leptocera* outnumbered the chironomids and that they were observed to pupate within the upper portions of the pitcher leaves.

Thanikaimoni, G. and G. Vasanthy. 1972. Sarraceniaceae: palynology and systematics. *Pollen et Spores* 14(2): 143-155.

Thanikaimoni and Vasanthy examined the pollen grains of 11 species in the Sarraceniaceae including *Darlingtonia*. Characters studied included number of apertures and dimensions of the exine, polar axis and equatorial axis. Excellent photographs of pollen grains are included. The authors suggest that the Sarraceniaceae may be closely related to the Ranunculaceae and Papavaraceae due to similarities in pollen morphology, as well as additional similarities of their flowers and habit.

Torrey, J. 1853. On the *Darlingtonia californica*, a new pitcher-plant from northern California. *Smithsonian contributions to knowledge* 6: 3-7.

Torrey's original monograph on *Darlingtonia*. This is the first known paper published on the species. He notes its discovery in 1842 near Mount Shasta. However, due to the lateness of the season, no flowers were found and so his official description was delayed until 1851 when a Dr. Hulse provided a specimen in flower. Torrey

immediately recognized it as a member of the Sarraceniaceae and had decided it was distinct from any existing genera in that family by the foliage alone. A detailed habitat and species description is provided. Torrey speculates on the affinity of the family to others, noting that his colleagues feel it is most closely related to the Nymphaeaceae and Papavaraceae.

Trappe, J. and J. Gerdemann. 1974. A northern extension of the range of *Darlingtonia*. Madrono 22:279.

This short piece describes the habitat characteristics of a *Darlingtonia* site near Sand Lake, Tillamook County, Oregon discovered by the authors. This site is 100 kilometers north of any previously recorded site as of 1970.

Viola, H. and C. Margolis (eds.). 1985. Magnificent voyagers: The U.S. Exploring Expedition, 1838-42. Smithsonian Institution. 303 pp.

Viola and Margolis describe the four year journey of the earliest American-led world exploring expedition, of which its most prized find was *Darlingtonia* discovered near Mount Shasta, California, in the fall of 1841.

Ziemer, R. 1973. Some field observations of *Darlingtonia* and *Pinguicula*. Carnivorous Plant Newsletter 2(2): 25-27.

Ziemer reports on four field sites he visited in the area of Gasquet, California. He found that the habitat conditions where these two species were found were quite diverse in slope, aspect and solar radiation, while all shared the characteristics of being located on Mesozoic ultrabasic intrusive rocks and having a constant, even supply of water. Ziemer noted differences in microhabitat between the two species and determined that “in this region the habitat requirements of *Pinguicula* seemed to be more exacting than that of *Darlingtonia*.”