Phytophaga, XIV (2004): 299-305
I S S N: 0393 - 8131

Biology of *Sarraceniopus darlingtoniae* (Histiostomatidae: Astigmata), an obligatory inhabitant of the fluid-filled pitchers of *Darlingtonia californica* (Sarraceniaceae)

NORMAN JAMES FASHING

Summary

Darlingtonia californica is a carnivorous plant with a patchy distribution in coastal Oregon and northern California, USA. A number of arthropod species inhabit and exploit its fluid-filled pitchers; among these is a hististomatid mite, *Sarraceniopus darlingtonia*, an obligate inhabitant that feeds on the rich microbial growth associated with decomposing arthropods captured by the pitcher. Males seek out and clasp tritonympal females, guarding them from other males by means of an enlarged second pair of legs. Upon molting, mating takes place. Eggs are laid on the pitcher wall above the fluid line, and, upon hatching, larvae move under the fluid. While larvae and protonymphs remain submerged, other instars can be found both below and above the pitcher fluid. Development from egg to adult is approximately nine days at 20ºC and six days at 25ºC. Mites overwinter as deutonymphs, with the first non-deutonymphal instars found in mid-March. Dispersal to newly forming pitchers on the same plant or closely adjacent plants is through ambulatory activity of deutonymphs rather than phoresy.

Key words: Sarraceniopus, Darlingtonia, phytotelmata, pitcher plant.

Introduction

In recent years phytotelmata have been praised as excellent subjects for testing community theory since they harbor arthropod communities and are natural microcosms that contain relatively few species, can be easily manipulated, and provide for replication. To date, such communities have been used to investigate local and regional variation in food web structure, the meaning of food web patterns, and predation and competition in patchy habitats (see Kitching, 2000 for review). Although mites are common inhabitants of phytotelma, often occurring in large numbers, little is known con-

Contribution of the 5th EURAAC - Symposium, Berlin 2004.

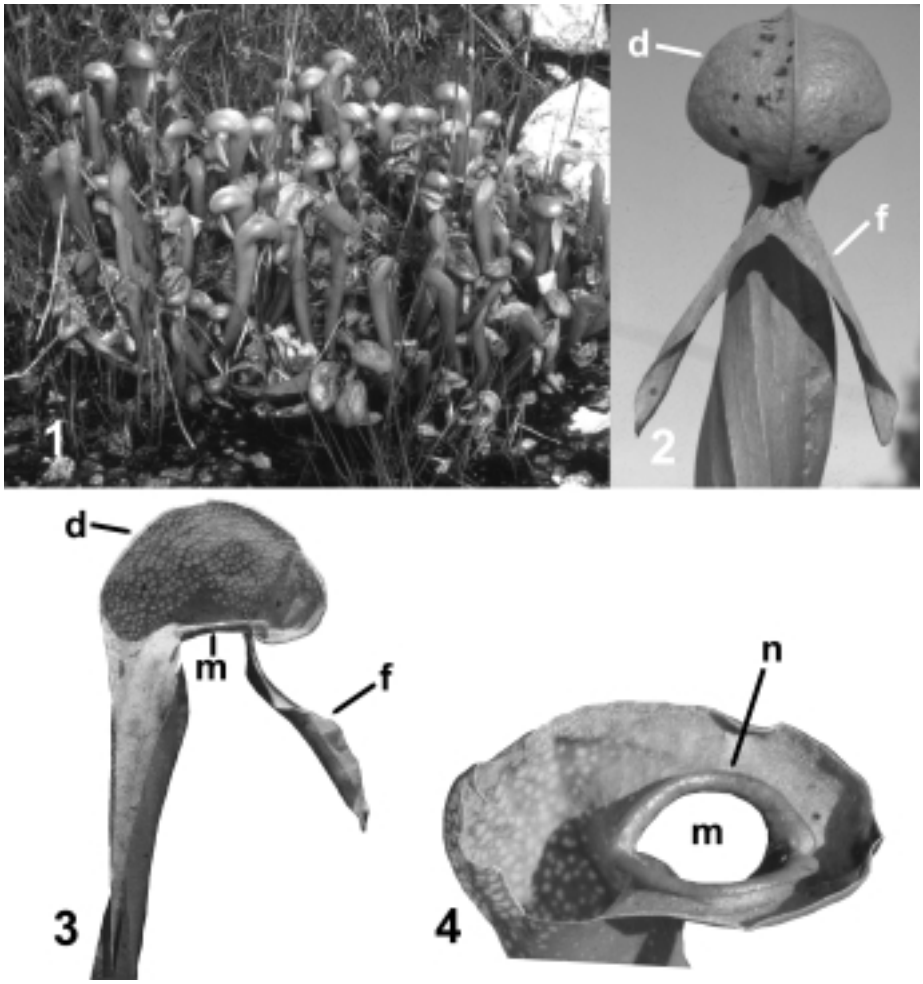
cerning the biology of most species. Mites may be small and difficult to study, but sheer numbers more than compensate for their lack of size. An understanding of the roles that various mite species play in phytotelm communities is therefore essential for an understanding of food webs and community dynamics. To date, arthropod communities found in the fluid-filled pitchers of *Darlingtonia californica* Torrey (Sarraceniaceae) have been used to study resource heterogeneity (Naeem, 1988) and food web dynamics (Nielsen, 1990). This phytotelm community also contains a common mite inhabitant, *Sarraceniopus darlingtoniae* Fashing & OConnor (Histiostomatidae), with little known concerning its biology. The present paper provides an overview of the biology and life history of *S. darlingtoniae*.

Study Area and Methods

The primary study site was Darlingtonia Wayside, a State Park located on the Pacific coast in central Oregon. Fully formed adult pitchers were collected at weekly or biweekly intervals from mid-January to mid-June, 1981, and transported in upright position to the laboratory for examination under a stereo microscope. The arthropod species in each pitcher were inventoried, and their locations noted. Pitcher contents were placed in finger bowls and used to rear inquilines. Individual mites were reared at 20 and 25 + 1ºC in small polystyrene cells (14 mm in diameter, 8 mm high) filled with pitcher fluid. Freshly cut pieces of larval *Metriocnemis edwardsi* Jones, a chironomid fly that also inhabits pitchers, were added to each cell to stimulate microbial growth, the food source for *S. darlingtoniae*.

Results and Discussion

Plant habitat and distribution. *Darlingtonia californica* is a carnivorous plant with leaves adapted as pitchers for capturing arthropods. It can be found growing in wet streamside habitats and perennial seeps in western Oregon and northern California (fig. 7). Pitchers range from 10-100 cm tall, and an individual plant produces many in large clumps (fig. 1). A pitcher consists of an elongate tube that gradually broadens toward the top where it abruptly widens and forms a dome (figs 1-3). In a horizontal position beneath the dome is the pitcher "mouth", an opening with margins curving inward to form a "nectar-roll" (figs 3, 4). The "fishtail", a forked tongue-like structure containing nectaries, hangs from the front margin of the mouth (figs 2, 3). Soon after opening in late spring or early summer, adult pitchers begin attracting arthropods that are enticed into the mouth by the richly baited nectar-roll. When ready to depart, window-like areolae in the dome lead them upward, and various morphological adaptations of the pitcher cause them to loose foothold and fall into plant-secreted fluid at the pitcher's base. The fluid does not contain enzymes, and captured arthro-



Figs 1-4 - *Darlingtonia californica*. 1. Clump of pitchers demonstrating their close proximity. 2. Anterior view of upper portion of pitcher. 3. Longitudinal section through upper portion of pitcher. 4. Upper portion of pitcher with dome removed. d = dome, f = fishtail, m = mouth, n = nectar-roll.

pods decompose through microbial action (see Juniper *et al*., 1989 for details). With its abundant supply of decomposing arthropods, each pitcher forms an excellent phytotelm habitat that can exist for up to a year, with new pitchers forming yearly.

Mite distribution. Pitchers are colonized by a number of organisms, among them *S. darlingtoniae*, and form a decomposer based community that can only exist by colonizing newly-formed pitchers on a yearly basis. *Sarraceniopus darlingtoniae* was collected from Darlingtonia Wayside and vicinity in Lane County, Oregon, and in California at Butterfly Valley

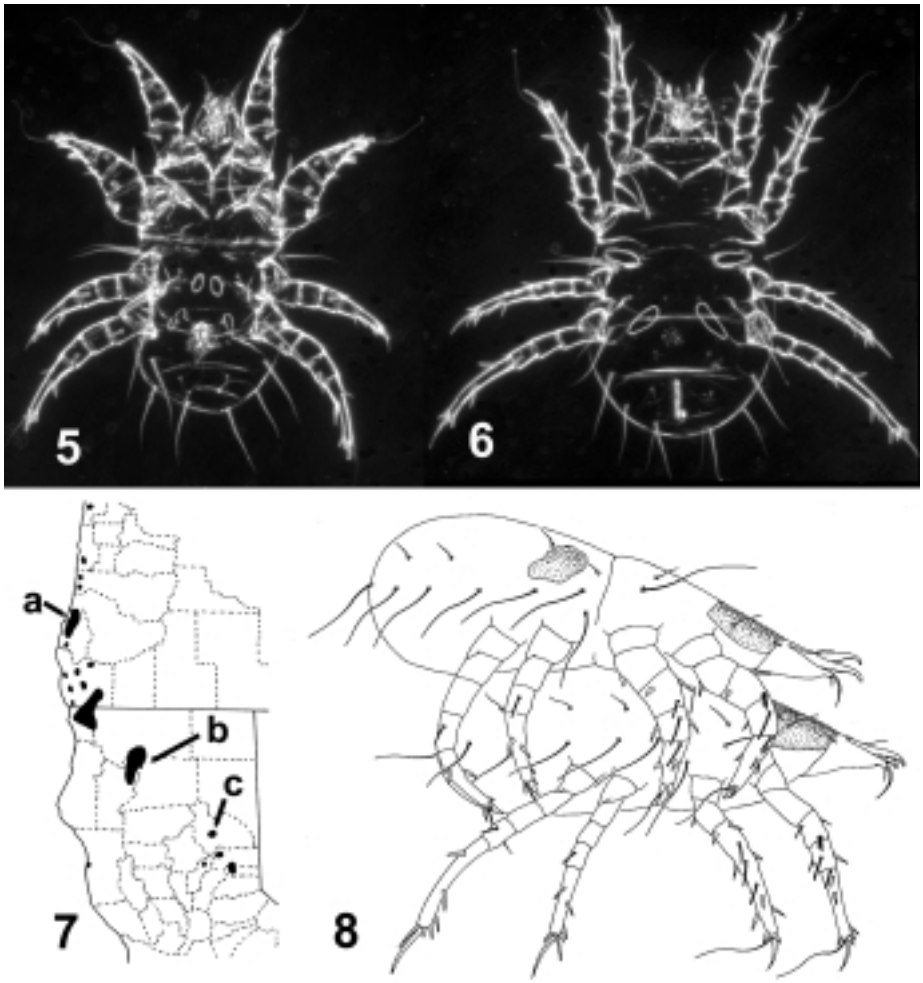
Botanical Reserve, Plumas County, and Gum Boot Lake, Siskiyou County (fig. 7). It has also been recorded from Del Norte County, California (Nielsen, 1990), and from the southern most populations of *D. californica* in Nevada County, California (Naczi, pers. comm.). *Sarraceniopus darlingtoniae* is most likely present in pitchers of *D. californica* throughout its range. Virtually every pitcher harbors *S. darlingtoniae*, with all instars being found beneath the fluid where trophic instars filter-feed on the rich microbial growth associated with decomposing arthropods. Deutonymphs, and occasionally adults and tritonymphs, can also be found on the pitcher wall above the fluid.

Mating and reproduction. Males seek female tritonymphs and actively guard them from other males. If another male tries to claim a female, the attendant male will push him away using his enlarged second pair of legs (fig. 5). Mating occurs upon tritonymphal ecdysis. Successful mate guarding insures paternity of resultant offspring since it prevents other males from gaining access to a virgin female. Males are highly attracted to female tritonymphs and virgin females, but cease guarding them shortly after mating. They show almost no interest in previously mated females, and it is probable that females mate only once. Males can readily distinguish quiescent females from quiescent males; of 27 tritonymphs guarded by males, 26 molted to reveal they were female. The guarding copulatory position of *S. darlingtoniae* males (fig. 8) is similar to that observed by Wurst and Kovac (2003) for *Tensiostoma veliaphilum* Wurst & Kovac. Legs I clasp the female's idiosoma between legs I and II, legs II between female legs II and III, legs III posterior to female legs IV and legs IV curve around the posterior of the female's idiosoma. If the male is small compared to the female, male legs III may clasp the female between legs III and IV.

As in other histiostomatids, *S. darlingtoniae* is arrhenotokous with unmated females producing only male offspring. Although the results from rearing 85 individuals were female biased (50 females vs. 35 males), the sex ratio did not differ significantly from 1:1 ($\chi^2 = 2.647$; df = 1; p = 0.104).

Life history. *Sarraceniopus darlingtoniae* overwinters in the deutonymphal stage, and is found on arthropod remains in the fluid as well as on the sides of the pitcher above the fluid line. The first non-deutonymph instars were collected on March 15, and trophic instars soon became dominant in mite populations. Deutonymphs, however, were always present in the pitchers. Laboratory studies indicate that the life cycle is quite rapid, with the development time from egg to adult 9.17 and 5.61 days at 20 and 25ºC respectively (tab. 1). The difference in development time between males (9.16 days at 20ºC; 5.40 at 25ºC) and females (9.18 days at 20ºC; 5.70 at 25ºC) was not significantly different at either temperature, but development time was significantly longer at 20ºC (t = 24.7; df = 83; p < 0.0005). Mites must colonize new pitchers each year, and rapid development allows them to quickly populate a new pitcher.

Of 80 deutonymphs collected from pitchers and placed in cells at 25ºC, 10 did not develop further. For the remaining 70, the mean development



Figs 5-8 - *Sarraceniopus darlingtoniae*. 5. Male; note enlarged legs, especially legs II. 6. Female. 7. Distribution of *D. californica* (black areas) and therefore *S. darlingtoniae*, in coastal Oregon and northern California; letters indicate collection sites (a = Darlingtonia Wayside, b = Gum Boot Lake, and c = Butterfly Valley). 8 Guarding/copulatory position of male.

time before entering quiescence was 5.2 days and the mean duration of the tritonymphal stage was 1.84 days. The mean quiescent period for molting deutonymphs was 1.05 days and that for molting tritonymphs 1.02 days. The inclusion of a deutonympal stage in the life cycle therefore prolongs tritonymphal development and quiescence (see tab. 1 for comparison).

Dispersal. *Darlingtonia californica* forms new pitchers in late spring and early summer, and old pitchers die. Inquilines must therefore colonize new pitchers on a yearly basis. All evidence indicates that *S. darlingtoniae* disperses to newly-opened adjacent pitchers on its own accord rather than

Table 1 - Duration, in days, of the life cycle stages of *S. darlintoniae*, egg through adult, reared on microbes associated with, and contents of, crushed fresh *M. edwardsi* larvae at 20 + 1ºC and 25 + 1ºC. n = sample size, R = range, M = mean, s.e. = standard error, LQ = larval quiescence, Proto = protonymph, PQ = protonymphal quiescence, Trito = tritonymph, TQ = tritonymphal quiescence, and To Adult = duration from egg to adult.

		Egg	Larva	LQ	Proto	PQ	Trito	TQ	To Adult
	n	53	47	45	35	33	33	33	53
	R	2.0-4.0	1.0-3.0	1.0-1.0	1.0-3.0	1.0-1.0	1.0-1.0	1.0-1.0	8.0-11.0
20°C	M	2.245	1.787	1.000	1.257	1.000	1.000	1.000	9.170
	s.e.	0.0655	0.0676	0.0000	0.0854	0.0000	0.0000	0.0000	0.0998
	n	32	31	32	21	18	18	26	32
	R	1.0-1.0	0.5-1.5	0.5-1.0	0.5-2.0	0.5-0.5	0.5-1.0	0.5-1.0	4.5-6.5
25°C	M	1.000	1.065	0.510	1.024	0.500	0.667	0.615	5.609
	s.e.	0.0000	0.0505	0.0153	0.0543	0.0000	0.0572	0.0421	0.0832

via phoresy. Unopened pitchers were marked on June 9, and revisited a week later. Of thirteen that had opened during the seven day interval, 12 (92%) contained mites whereas only 5 (39%) contained midge larvae, the only other arthropod species present. Mites therefore colonized newly opened pitchers earlier than midges and dispersed by walking. This has been confirmed by Dr. Robert Naczi (pers. comm.) who has observed such short-distance dispersal behavior in *S. darlingtoniae* as well as in *S. gibsoni* (Nesbitt), an inhabitant of the pitchers of *Sarracenia purpurea* L. Deutonymphs leave the old pitchers, walk to newly forming adjacent pitchers where they congregate at the leaf tips, and enter the new pitchers when they open. He too found that deutonymphs extracted from old pitchers and reared in the lab had a prolonged life cycle as discussed above; however, he also found that those dispersing to new pitchers did not share this attribute and progressed rapidly to the adult stage once inside the new pitcher. Of the 70 deutonymphs reared to adults as discussed above, 62 (88.6%) were female and only 8 (11.4%) male, indicating that dispersal in *S. darlingtoniae* is primarily accomplished by female deutonymphs.

The mechanism for dispersal between *D. californica* clumps in the same locality as well as long-distance dispersal to *D. californica* populations elsewhere is unknown. Deutonymphs were not found on insects in field collections, but they did on occasion attach to the flies *M. edwardsi* and *Megaselia orestes* Borgmeir in the lab. It is possible that these two fly species are used for long-distance dispersal, however neither species appears to be a strong flier.

Acknowledgements

I am grateful to Dr. G W Krantz and the Entomology Department of Oregon State University for providing laboratory space for this research, to Mr. J Davis,

State of Oregon Park Service, for permission to collect cobra lily pitchers at Darlingtonia Wayside, to Mr. G Stores, Eugene, Oregon, for permission to collect cobra lily pitchers on his property, and to Dr. R Naczi, Delaware State University, for sharing his unpublished observations on *Sarraceniopus* species and for his critical review of the manuscript.

References

JUNIPER B., ROBBINS R, JOEL D. - 1989 - The carnivorous plants. - *Academic Press*, 353 pp.

KITCHING R. - 2000 - Food webs and container habitats. - *Cambridge Univ. Press*, 431 pp.

NAEEM S. - 1988 - Resource heterogeneity fosters coexistence of a mite and a midge in pitcher plants. - *Ecol. Monogr.*, 58: 215-227.

NIELSEN D. - 1990 - Arthropod communities associated with *Darlingtonia californica*. - *Ann. Entomol. Soc. Am.*, 83: 189-200.

WURST E., KOVAC D. - 2003 - Description and biology of the mite *Tensiostoma veliaphilum* n. gen. n. sp. from the water surface of bamboo phytotelmata in Southeast Asia (Aranchnida, Acari, Astigmata, Histiostomatidae). - *Senckenb.Biol.*, 82: 63-98.

Author's address

N.J. FASHING - Department of Biology, College of William and Mary, Williamsburg, VA 23187-8795 (USA).