

Thirty Years Research on Vernal Pool Macroinvertebrates from Vina Plains

DOUGLAS G. ALEXANDER

Department of Biological Sciences, California State University, Chico, CA 95929
dalexander@csuchico.edu

ABSTRACT. This review combines thirty years of irregular observations on California vernal pool invertebrates with a series of independent student research projects influenced by my interests. The material reviewed was published between 1970 and 1997, unified by a common focus on pools found at Vina Plains, an area in southern Tehama County, now preserved by the California Nature Conservancy. This relatively level landscape has internal basins forming a diverse assemblage of vernal pools dependent upon rain and flooded for variable times in the winter but dry every summer. Climate patterns for the 54 years between September 1951 and May 2005 were added to this discussion. Rainfall was highly variable from month to month and from year to year with occasionally high rainfall events between January and March resulting in higher seasonal totals. Flooding and drying times for twenty pools during all or part of thirteen different rainy seasons between 1967 and 1995 were extracted from the papers reviewed. The length of the aquatic phase was variable and highly reduced or incomplete in drought years. Pools form rarely in October, occasionally in November and more commonly in December and January and rarely in February. Aspects of the life history patterns of the vernal pool snail (*Fossaria sonomensis*), conservancy fairy shrimp (*Branchinecta conservatio*), vernal pool fairy shrimp (*Branchinecta lynchi*), California linderiella (*Linderiella occidentalis*), vernal pool tadpole shrimp (*Lepidurus packardii*), California clam shrimp (*Cyzicus californicus*), and two common planktonic copepods (*Leptodiaptomus tyrrelli* and *Hesperodiaptomus eiseni*) were considered. Field observations established predation on fairy shrimp by a common Notonectid predator (*Notonecta kirbyi*). Several insects and their young were important predators in the pools; however, many should be considered accidentals because they rarely complete reproduction before drydown. The vernal pool snail required more than one year to complete reproduction, surviving the summer aestivating within the sediments. The crustaceans survived the summer as a diapausing cyst. The high abundance of the California clam shrimp observed in the 1970's was not observed in the 1990's. The largest pools represent major cyst banks for the conservancy fairy shrimp and the vernal pool tadpole shrimp. The conservancy fairy shrimp had dense populations in the largest pools but was also found in medium sized pools. California linderiella was common in many pools except the largest pools and the vernal pool fairy shrimp was found in smaller populations in small pools that dry early. The vernal pool fairy shrimp, vernal pool tadpole shrimp and small copepod (*Leptodiaptomus tyrrelli*) potentially had multiple generations during one pool season and the others had a single generation. Maintenance of vernal pool invertebrates requires preserving landscapes with diverse pools where annual and seasonal variability is preserved.

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INTRODUCTION

Vina Plains vernal pool landscape is a piedmont bench extending south from Deer Creek, in the Sacramento River Valley, in southern Tehama County, California. This relatively level landscape has internal basins that concentrate rainwater into depressions. The temporary pools produced (California vernal pools) represent the above-ground part of a perched water table that accumulates above an impervious soil layer. Pools range from surface puddles, a few square meters in area, flooding and dry-

ing several times during one rainy season, to larger pools on clay soil that typically hold water for three to six months. In the spring, the waterlogged soils exposed by drying pools support amphibious flora. The pools and surrounding grasslands have spectacular spring flower displays followed by a dry and hot summer.

I still remember the feelings I had watching the dry plains transform into a vibrant pool landscape in fall 1965. This area was a destination for class and small group field trips and several graduate students

developed thesis projects centered on vernal pool invertebrates. Alexander (1976) provides an early review of these activities. Vernal pool research increased after The Nature Conservancy (TNC) purchased Vina Plains Preserve (VPP) in 1982.

The presence and depth of water in the pools is unpredictable from year to year. Pool invertebrates must withstand variability in pool flooding and reproduce before the loss of standing water. Some of the vernal pool invertebrates are rare as are some plants found only on pool floors in the summer (Alexander and Schlising, 1997, 1998; Schlising, 2007).

A vernal pool snail and crustaceans, including the large and easily recognizable fairy shrimp, tadpole shrimp and clam shrimp, display distinctive life history patterns in these pools. Pools are also annually invaded by insects, some of which complete development before pool drydown. A variety of adaptations allow invertebrates to reproduce in pools and survive the dry summer in resistant stages. General climate patterns, also reviewed in this paper, influence invertebrate life history patterns that vary both from year to year and from large to small pools.

PAPERS REVIEWED, SPECIES CONSIDERED AND TECHNIQUES USED

This paper combines my research and personal observations with that of graduate students (Table 1), and unpublished material. Michener, Wolt, Lanway, Ahl, Patton, Gallagher, Syrdahl, Ballantyne, and Kirn completed graduate degrees under my chairmanship. Newman and Eads worked under the chairmanship of Robert E. Thomas and Jeffrey Bell. Unpublished information was obtained from the students listed above and undergraduate research by Wendy Marsters Appell. The work by Alexander and Schlising (1997 and 1998) was supported by U. S. Fish and Wildlife Service Section 6 funds (Contract Number FG 4506-R1) that came to us through The California Department of Fish and Game. The pools studied are identified in Figure 1. After 1995, my collections and those done by Kirn were controlled by the appropriate federal and state permits.

Michener (1970), Wolt (1972), Ahl (1983) and Ballantyne (1994) researched specific vernal pool crustaceans. Newman (1973) and Gallagher (1992) researched vernal pool snails. With the exception of a summary figure in Michener (1970), references targeting specific species did not include comments

about other invertebrates. Syrdahl (1993) considered all large invertebrates caught in biweekly collections from 14 large pools during 1991-1992. Patton (1984) compared *Linderiella occidentalis* with an unidentified *Branchinecta* which turned out to be two species. Lanway (1974) considered hatching of select crustaceans. Syrdahl included insects, generally identified by higher taxa, and Kirn (1997) studied predation of the backswimmer, *Notonecta kirbyi*.

Lanway (1974) and Patton (1984) did not distinguish the two species of *Branchinecta* (*B. conservatio* and *B. lynchi*, see Eng et al., 1990 and Eriksen and Belk, 1999) reducing the usefulness of their references to this genus. The calanoid copepods, *Leptodiptomus tyrrelli* and *Hesperodiptomus eiseni* were identified by Janet Reid (Ballantyne, 1994); Michener, Lanway and Syrdahl used the same specific names in the genus *Diptomus*. The clam shrimp, *Cyzicus californicus*, was called *C. mexicanus* in Michener, Wolt and Lanway. Gallagher contains a synonymy of the vernal pool snail, *Fossaria sonomensis* that was called *Bakerilynaea cockerelli* by Newman.

Field and laboratory methods are summarized in Table 2. Original papers should be consulted for details. Invertebrates were collected in nets that pick up a mix of planktonic and benthic organisms. Wolt, Ahl and Syrdahl increased the number of benthic organisms by pulling the net rapidly through the water and reversing the net direction to cover the same area, collecting organisms drawn from the sediments by the first pass. Alexander and Gallagher pulled nets set distances through specific habitats using the number of individuals collected to develop density indices.

VINA PLAINS, A CALIFORNIA VERNAL POOL LANDSCAPE

Location

Vina Plains vernal pool landscape is 30 km north of Chico. Highway 99 traverses this area north of the county line between Butte and Tehama Counties (Figure 1). This landscape is bordered on the south and west by younger flood plain soils supporting orchards. To the north, agricultural activity uses surface irrigation water from Deer Creek. Singer Creek forms the eastern edge of this area with similar landscape to the east joining the foothills. The initial tract of Vina Plains Preserve forms a triangle pointing south with Lassen Road on the north and

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TABLE 1. References used in this review, with a list of species considered, pools studied and years of study.

Reference	Species considered ¹	Pool(s) studied ²	Time of study
Michener (1970) ³	<i>Leptodiaptomus tyrrelli</i> , small copepod <i>Hesperodiaptomus eiseni</i> , large copepod	A	1967-1968
Wolt (1972) ³	<i>Cyzicus californicus</i> , clam shrimp	A[2]; B[1]; C[4]; 1[3]; south of Chico[5]	1970-1971 1971 spring 1971-1972
Newman (1973)	<i>Fossaria sonomensis</i> , vernal pool snail	[North-east of Vina Plains]	1972, 1973
Lanway (1974) ³	Fairy shrimp, not identified to species <i>Lepidurus packardi</i> , vernal pool tadpole shrimp <i>Cyzicus californicus</i> , clam shrimp <i>Leptodiaptomus tyrrelli</i> , small copepod <i>Hesperodiaptomus eiseni</i> , large copepod	A[1]; B[2]; C[4]; 1[3]; south of Chico[5]	1972-1973, 1973 fall
Ahl (1983) ³	<i>Lepidurus packardi</i> , vernal pool tadpole shrimp	A [I]; a [III]; B [II]	1980 to 1982
Patton (1984)	<i>Linderiella occidentalis</i> , CA fairy shrimp Two species of <i>Branchinecta</i> not separated	A and pools throughout area	1981 to 1983
Gallagher (1992) ³	<i>Fossaria sonomensis</i> , vernal pool snail	major pools on VPP Field trials in 35; 36	1989 spring Through 1991 spring
Syrdahl (1993) ³	<i>Fossaria sonomensis</i> , vernal pool snail <i>Branchinecta conservatio</i> , conservancy fairy shrimp <i>Branchinecta lynchi</i> , vernal pool fairy shrimp <i>Linderiella occidentalis</i> , CA fairy shrimp <i>Lepidurus packardi</i> , vernal pool tadpole shrimp <i>Leptodiaptomus tyrrelli</i> , small copepod <i>Hesperodiaptomus eiseni</i> , large copepod 36 additional taxa	1; 14; 16; 17; 18; 21; 22; 29; 34; 35; 36; 37; 38; 39	1991-1992
Ballantyne (1994)	<i>Hesperodiaptomus eiseni</i> , large copepod	Sampled 17; 21; 35	1991 to 1993
Eads (1995)	<i>Branchinecta conservatio</i> , conservancy fairy shrimp	35; (Olcott Pool, Jepson Prairie Preserve)	1994 spring
Kirn (1997)	<i>Notonecta kirbyi</i> , back swimmer	Sampled 14; 16; 17; 34; 35; 36 Feeding trials 14; 16; 34; 35; 36	1995 spring
Alexander and Schlisling (1997 and 1998) ³	<i>Branchinecta conservatio</i> , conservancy fairy shrimp <i>Linderiella occidentalis</i> , CA fairy shrimp <i>Lepidurus packardi</i> , vernal pool tadpole shrimp <i>Cyzicus californicus</i> , clam shrimp	1; 14; 16; 17; 18; 21; 22; 29; 30; 34; 35; 36; 37; 38; 40; 41; 42	1995 spring

¹ Accepted nomenclature, some authors used different nomenclature.

² Refer to Figure 1. Letter designations for pools north of the initial tract of Vina Plains Preserve. Number designations for pools on the initial tract of Vina Plains Preserve (King, 1992). Brackets indicate pool designations by authors. Pools studied south of Chico excluded from this paper.

³ References that contain information on pool hydroperiods (see Table 4).

Highway 99 and Singer Creek adjacent to the other sides (Figure 1).

The papers reviewed considered pools along Leininger Road (Pools A, a, B), a pool north of Lassen Road west of Singer Creek (Pool C) and pools on VPP, using pool numbers established by King (1992) (Table 1 and Figure 1). Leininger Road was initially called Keefer Road, an unimproved gravel road with a sign warning individuals not to traverse pools flooding the road. Road improvement in-

cluded a culvert placed where the road crossed Pool A. The road and culvert separated a small eastern pool (Pool a) from Pool A during most of the wet season.

Land Use

The initial tract of Vina Plains Preserve was purchased in 1982 by The Nature Conservancy as part of the Critical Areas Program preserving unprotected native ecosystems in California. TNC provided

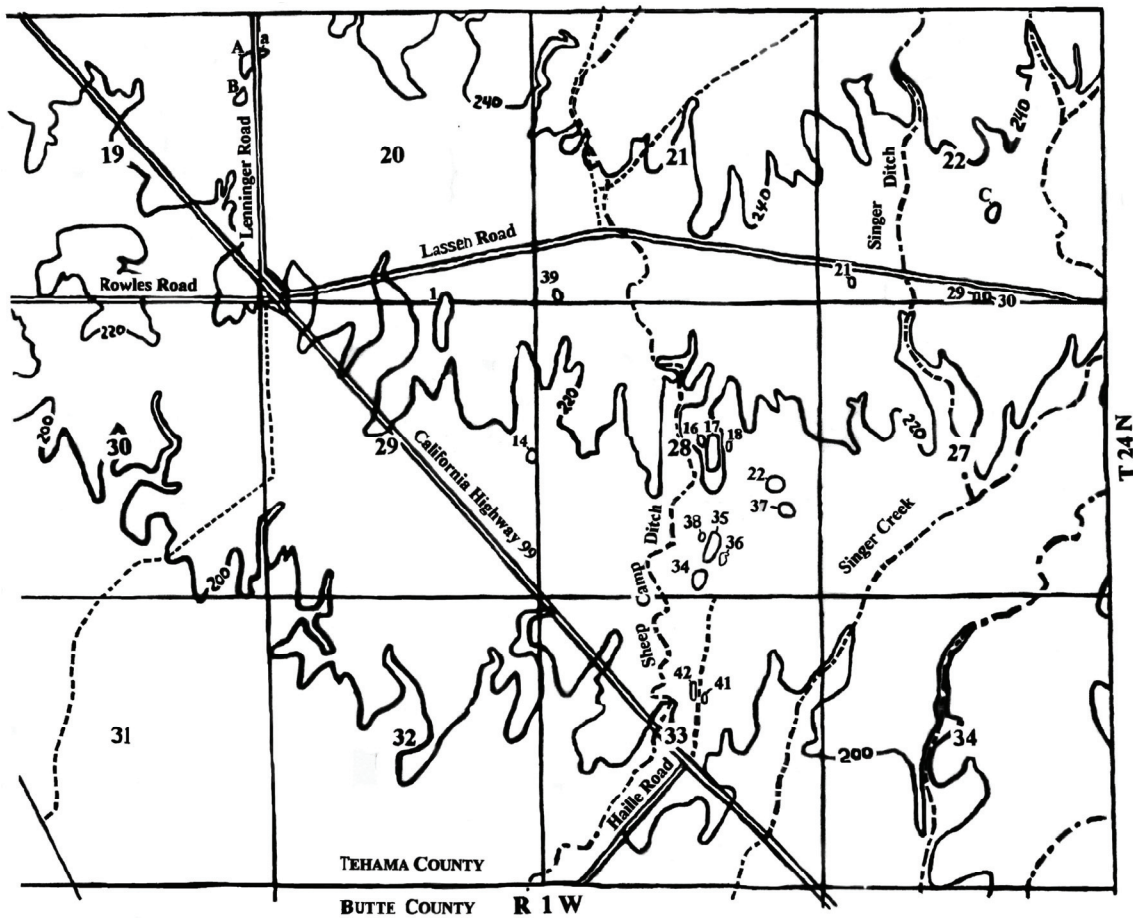


FIGURE 1. Vina Plains vernal pool landscape, with pools studied in 1960 to 1980 identified by letters and pools studied in 1980 to 1990 on the initial tract of Vina Plains Preserve identified by small numbers (King, 1992). The large numbers are section numbers representing twelve one mile square sections in the south west corner of T 24 N, R 1 E. Additional pools currently preserved by TNC and not identified in this figure are located west of Highway 99 and north of Lassen Road.

stiles for access to the vernal pool landscape along the south side of Lassen Road and removed a barn located within the initial unit. They also purchased additional tracts west of Highway 99 (including the Wurlitzer Tract in Butte County) and added a major conservation easement north of Lassen Road and east of Highway 99. This action has preserved much of this vernal pool landscape that now is in the south-western edge of the Lassen Foothills Project. A strip of land east of VPP (including Singer Creek) extending from Lassen Road to Highway 99 was purchased by CalTrans for mitigation.

Other than the roads, land modifications at the west junctions of Highway 99 with Haille and Rowles Roads include a livestock barn, orchards and a nut-processing plant. Development has compromised the native landscape along Rowles Road between Highway 99 and orchard land to the west. A ranch house and associated barns (derived from an early

sheep camp) are located north of Lassen Road adjacent to Sheep Camp Ditch.

Two natural channels, potentially augmented by Deer Creek water, cross VPP (Sheep Camp Ditch and Singer Ditch). A dam on Sheep Camp Ditch was removed as part of a water use settlement. Singer Ditch has an earthen dam that was breached by high water events changing the route of the natural channel. The dam has not been removed and some water accumulates behind it during the rainy season.

This landscape has been used as winter and spring range land for many years. Cattle are observed in the pools, especially in hot weather toward the end of the pool season, just before the cattle are removed. The landscape management plan of TNC preserves vernal pools and rotates fire and seasonal

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TABLE 2. Methods used to study vernal pool invertebrates on Vina Plains.

Field and laboratory methods	References
Use of a chronological series of field-preserved collections to study:	
Life history changes of:	
two species of calanoid copepods	Michener (1970)
clam shrimp	Wolt (1972)
tadpole shrimp	Ahl (1983, 1991)
fairy shrimp	Patton (1984)
Presence or absence of large invertebrates in 78 biweekly collections in 14 vernal pools	Syrdahl (1993)
Use of a chronological series of non-lethal field collections to study:	
vernal pool snails	Gallagher (1992, 1993)
large branchiopod crustaceans in small pools	Marsters, undergraduate research
large branchiopod crustaceans in larger pools	Alexander and Schlising (1997, 1998)
Field tests to study:	
snail growth and fecundity in adjacent pools	Gallagher (1992, 1993)
backswimmer predation on Anostraca and water boatmen	Kirn (1997)
Laboratory study of live collections to consider:	
condition of aestivating snails	Newman (1973), Newman and Thomas (1975)
vernal pool snail growth and fecundity	Gallagher (1992, 1993)
vernal pool snail parasite load	Eads, personal communication
cyst hatching of large branchiopods and calanoid copepods	Lanway (1974)
tadpole shrimp growth, cyst deposition and hatching	Ahl (1983, 1991)
clam shrimp hatching, growth and behavior	Wolt (1972)
copepod feeding dynamics using video microscopy	Ballantyne (1994)
Special field fixation for	
DNA analysis of conservancy fairy shrimp	Eads (1995)
scanning electron microscopy of large copepod	Ballantyne (1994)

cattle grazing between different units. Pools 18, 29, 42 and part of 22 have been fenced to exclude cattle.

Topography

Vina Plains is a mid Pleistocene alluvial fan that gently slopes to the south and drops off abruptly at the connection between the older soils of the alluvium with the younger flood plain soils of Singer Creek and the Sacramento River. This landform originated by alluvial deposits from Deer Creek. The vernal pools are on a relatively level landscape (60 to 75 m above sea level) that has incised drainage channels. The displacement of these channels from the foothills and their north-south orientation distinguishes this landscape from vernal pool landscapes near Chico (Andrew E. Conlin, NRCS, Soil Survey Project Leader, personal communication).

Fall and winter rainfall and rainfall-runoff from limited mini-watersheds form pools in depressions that have an impervious subsoil layer. Pool size ranges from a maximum of over 30,300 m², through inter-

mediate size pools (15,000 to 25,000 m²) to numerous smaller pools. Larger individual pools have adjacent wetland soils contiguous with pool sediments. Pools are irregular, and adjacent pools often have independent mini-watersheds.

Climate and Pools

Pool formation depended upon rainfall that has displayed extremely different intensities and patterns during our field research. Daily rainfall and temperature values taken at the Red Bluff Airport (30 km north west of Vina Plains) for June 1951 through May 2005 (University of California Statewide IPM Program web site, 2006) were used to illustrate climate patterns.

Monthly minimum, mean and maximum rainfall values illustrate a rainfall season from September to May with little to no rainfall during summer (Figure 2). The total rainfall for June, July and August was never greater than 52 mm, and was zero for 15% of the 54 years. Monthly averages above 75 mm indi-

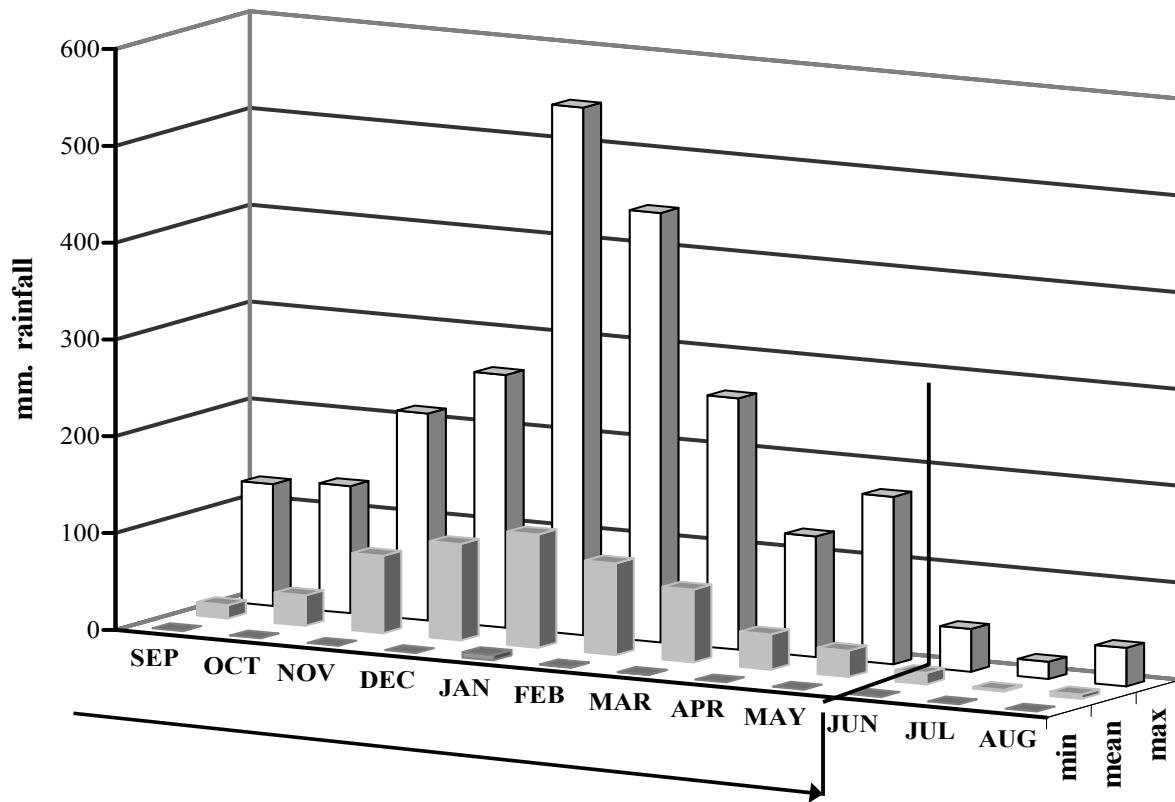


FIGURE 2. Monthly minimum, mean and maximum precipitation averaged for 54 years from September 1951 through May 2006 at Red Bluff Airport. The horizontal arrow indicates seasonal rainfall (September of year x through May of year x +1). Summer values represent trace rainfall occurring during the typically dry season.

cate the heaviest rains typically occur from November through March. Heavy rainfall is unpredictable with maximum monthly rainfall many times the mean and minimum values (which are at or near zero). Rains occur infrequently, with increasing average totals and greatly increasing maximum totals for September to January. Rain storms are less frequent, but potentially heavy in March, April and May. Pools occasionally form in October and November, more frequently in December and January and rarely in February. The time of pool drydown is variable, influenced by the increasing evaporation and less predictable rain. The total seasonal rainfall (September through May) ranged from a maximum over 1,300 mm (1997-1998) to a minimum under 240 mm (1975-1976) (Figure 3).

I determined cumulative daily rainfall for September through May from 1951 to 2005 that illustrates the importance of the time of rain as well as seasonal totals (Figure 4). In 54 seasons, the rains started as late as 30 November (1995) and there was no rain after 10 April (1982). The average seasonal rainfall midpoint was 15 January, and variability is illustrated by the earliest midpoint 22 November (1963-

1964) and the latest midpoint 3 March (1990-1991). The highest seasonal rainfall values result from heavy rain storms between January and March. The bulk of the yearly rainfall tracks fall below these high values. The lowest seasonal rainfall years were only slightly lower than the general rainfall pattern. The 1970's represented a very low rainfall period with three low rainfall years from fall 1971 through spring 1977.

Standing water that developed from early rains (e.g., 106 mm, 16-18 September 1989) (Figure 4) dried without more rain, illustrating the importance of including evaporation with rainfall patterns. (Attempts to use available evaporation data did not produce a useful pool flooding model.) The loss of deep cracks in clay soils before heavy rain indicated water input by dew must also be included in a more complete model of pool flooding. Late season rains, after pools are drying, have reduced impact on water depth. For example, May typically represents less than 5% of total seasonal rainfall; however, in 1976-1977 May rain was 20% indicating the seasonal total included rain that had little impact on pools.

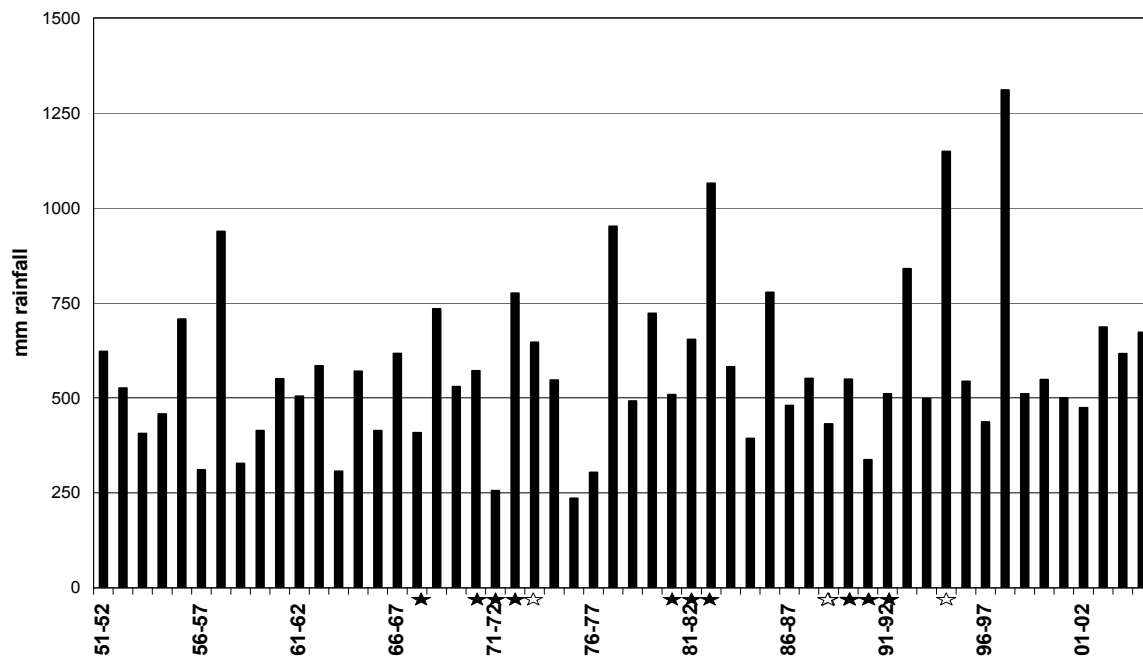


FIGURE 3. Seasonal (September through May) precipitation at Red Bluff Airport for September 1951 through May 2005. The mean precipitation for this time was 575 millimeters with the minimum 236 millimeters recorded in 1975-1976 and the maximum 1,310 millimeters recorded in 1997-1998. Closed stars indicate years when investigators reported on pool flooding and drydown. Open stars indicate years with incomplete observations.

Our field activities were conducted under potentially hot and cold conditions, illustrated by the monthly minimum and maximum temperatures from the Red Bluff Airport (Figure 5). The rapid drop in fall temperatures illustrates dew can occur before rains start and pool flooding will typically involve cold water temperatures. Although winter high (daytime) air temperature can be as high as 25° C, some days in December and January potentially remain below freezing all day when nets froze as they were taken out of the water. Maximum (day) temperatures increase as days become longer through March and April with a low probability of freezing (night) temperatures (Table 3). Although spring conditions do not favor pool retention, the air temperature increase is more gradual than the air temperature drop in fall. These air temperatures indicate that pools remaining into late spring and summer will have water temperature increases before drydown. The surface of summer pool sediments becomes extremely hot, potentially reducing cyst survival. I have recorded dry surface pool sediment temperatures over 50° C and Keeley and Zedler (1998) report dry vernal pool surface temperatures up to 70° C. Low minimum air temperatures in the summer indicate cold nights (similar to a desert).

Table 3, considering the 54 years, divides any one year into several parts, including a very hot period (June—September) with a higher probability of maximum temperatures exceeding 40° C and a cold period (November—February) with a higher probability of freezing temperatures.

Pool Characteristics

Temporary annual pool variation is influenced by year to year climate variation, introduced above, and by differences across the landscape. It is impossible to meaningfully refer to an average pool. Furthermore, adjacent pools have different and independent mini-watersheds. The range of pool types is supported by the different communities of spring flowers, including flowers blooming in shallow areas, bands of flowers around intermediate size pools and sheets of flowers on the dry floor of larger pools that also support unique plants in the summer (Schlising, 2007). These pool differences are also reflected by different life history stages and population densities of aquatic invertebrates.

Intermediate and large pools have clay sediments and high turbidity increased by wind-mixing. Reduced light penetration in these pools is supported

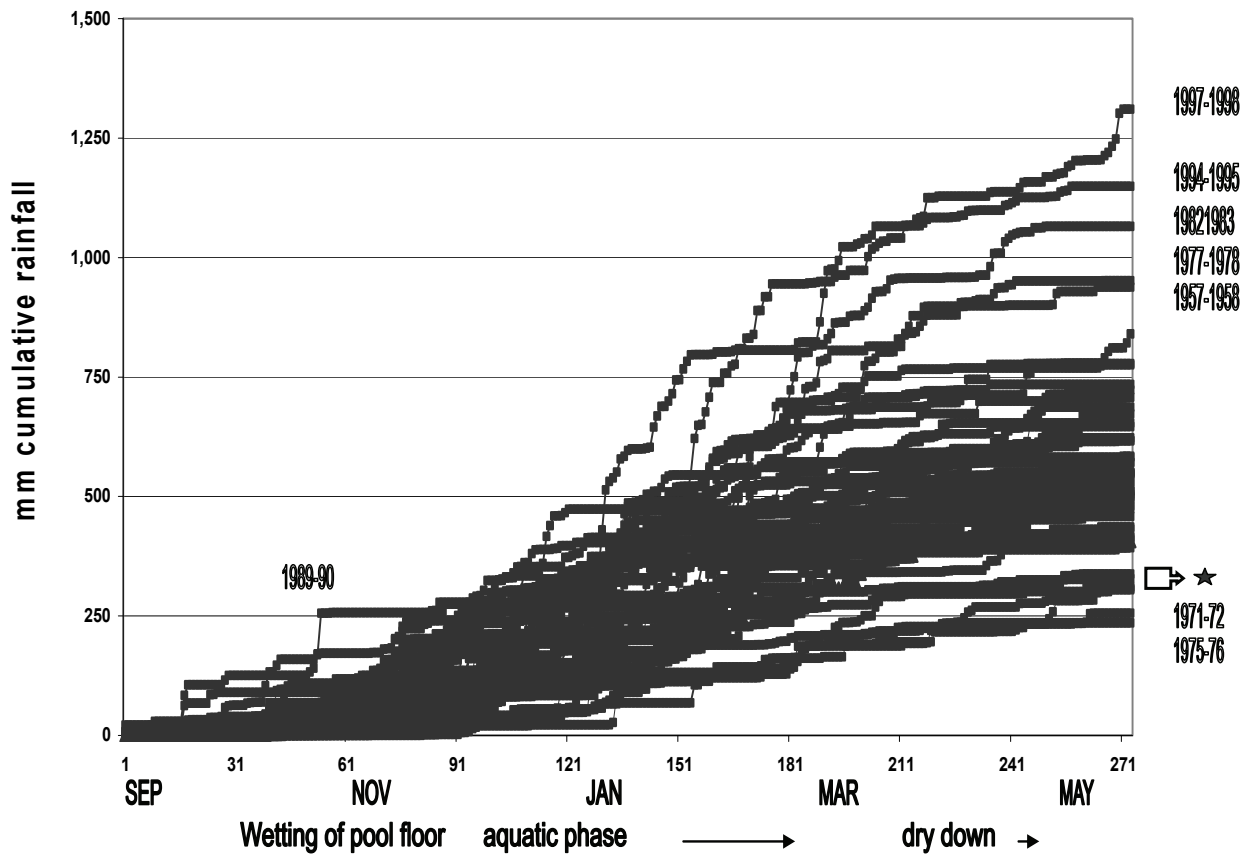


FIGURE 4. Cumulative seasonal rainfall (September 1 through May 31) for Red Bluff Airport for September 1951 through May 2005. Numbers represent cumulative days from September 1 (1) to May 31 (271). The 5 highest (938 mm and higher) rainfall years are listed. The 7 lowest (337 mm and lower) rainfall years, ordered by increasing total rainfall values were: 1975-1976, 1971-1972, and five years indicated by the star, 1976-1977, 1963-1964, 1956-1957, 1958-1959, and 1990-1991. The remaining 42 years had rainfall totals between 393 and 840 mm.

by the presence of aquatic plants that display floating leaves (e.g., *Marsilea vestita*).

I extracted general information from all appropriate references (Table 1) on flooding and drying times for twenty pools during all or part of thirteen rainy seasons between 1967 and 1995 (Table 4, Figure 1). Although these scattered observations cannot be used to determine the annual probability of pool flooding, they provide information on a range of dry to wet years including two of the lowest rainfall years and one of the highest rainfall years presented in Figure 3. The published work did not consider smaller pools (formed in clay and on surface hardpan).

The larger pools studied typically contained water for several months with extreme conditions ranging from slightly over one month to seven months (Table 4). Initial flooding was variable in both time of the year and time required to fill pool basins, not illustrated in Table 4. There is pronounced variability

in time of flooding in low rainfall years. Pool formation required hydration of clay soils that occurred either by rains or by dew before rains—indicated by the loss of soil cracks. October pool formation was observed in 1981 and 1982 (Ahl, 1983; Patton, 1984). November and December pool formation was common. With the exception of the drought years, 1971-1972 and 1990-1991, pools were flooded from January through March. Discontinuous periods of standing water with February flooding were observed during two low rainfall years, Pool 1 during 1971-1972 (Wolt, 1972) and Pool 35 during 1990-1991 (Gallagher, 1992). A rapid drydown occurred in most pools from early April to mid May. The two largest pools (Pools 1 and 17) held water longer with a July drydown recorded during 1995 (Alexander and Schlising, 1997).

Pools are astatic with rainfall input increasing water depth and evaporative loss decreasing depth. Maximum pool depth was typically controlled by seepage

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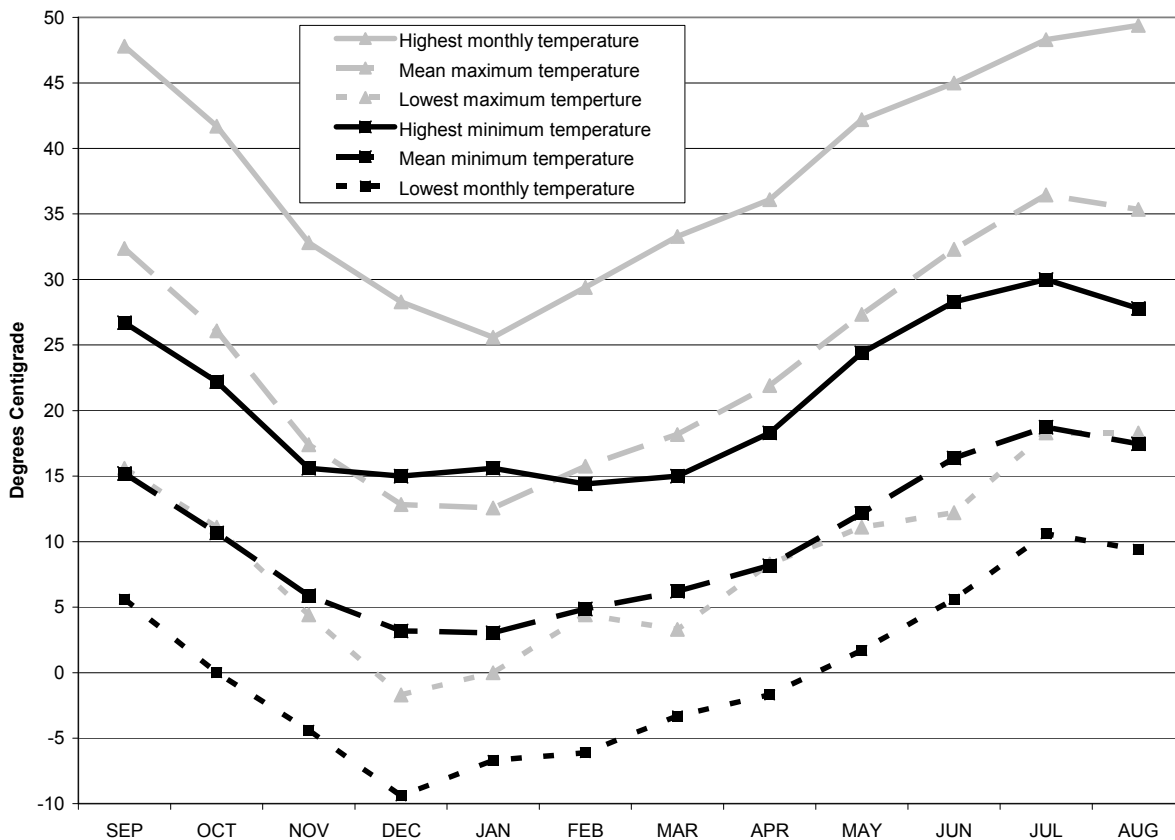


FIGURE 5. Monthly maximum and minimum temperatures for Red Bluff Airport for June 1951 through May 2005. The range between average maximum (daytime) temperatures and average minimum (nighttime) temperatures was 10 to 12 from November to March and 16 to 18 June to September. Highest monthly temperatures were never below 25 and were 45 or higher June through September. The time of pool flooding is a time of cold air temperatures. Compare with Table 3.

into adjacent clay soils that expand the wetland area beyond the water edge. As a result, this landscape retains high quantities of rain water. During De-

TABLE 3. The percent of days from 1951 through 2006 when Red Bluff airport maximum temperature was equal to or above 40° C, and the minimum temperature was equal to or below 0° C.

	≥ 40°	≤ 0°
SEP	5.2%	0.0%
OCT	0.4%	0.1%
NOV	0.0%	6.0%
DEC	0.0%	22.6%
JAN	0.0%	24.7%
FEB	0.0%	9.4%
MAR	0.0%	2.6%
APR	0.0%	0.6%
MAY	0.2%	0.0%
JUN	8.9%	0.0%
JUL	20.7%	0.0%
AUG	13.3%	0.0%

ember and January, temperatures are low and ice is more likely to form on water and wet sediments. Shallow pool water temperatures are influenced by daily air temperature changes whereas deeper pools have water temperatures that change gradually reflecting the influence of air temperatures of previous days and weeks. All pools have elevated temperatures and lower dissolved oxygen during drydown; however, during shallow pool drydown, deeper pools have lower water temperatures and more dissolved oxygen. Late in the pool season, the only remaining large pools have high water temperatures (20 to 30°C).

Syr Dahl (1993) observed the following pool differences in one season. 1) initial flooding occurred over 6 weeks—December to January. 2) The time of standing water ranged from 15 to 23 weeks. 3) Time of drydown occurred over 7 weeks—April to June. 4) Maximum pool size occurred over 9 weeks—January to March. 5) Surface areas ranged from 1,890 to 30,362 m².

TABLE 4. Hydroperiods of pools observed during invertebrate collections. Each unit represents slightly more than nine days. Standing water represented by "x." Blanks represent no standing water. Some of the dry periods following reflooding, were only five to seven days. The "--" indicates no observations for flooding or drydown were done.

Pool	Rain season	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	Reference
A	1967-1968			x	x x x	x x x	x x x	x x x	x x x					Michener
	1970-1971			x	x x x	x x x	x x x	x x x	x x x					Wolt (1972)
	1971-1972				x	x	x x x	x x x	x x x					Wolt (1972)
	1972-1973			x	x x x	x x x	x x x	x x x	x x x	x				Lanway (1974)
	1973-1974			x	x x x	x x x	x x x	x x x	--	--				Lanway (1974)
	1980-1981			x	x x x	x x x	x x x	x x x	x x x	x x				Ahl (1983)
	1981-1982			x	x x x	x x x	x x x	x x x	x x x	x x x				Ahl (1983)
	1982-1983		x	x	x x x	x x x	x x x	x x x	x x x	x x x				Patton (1984)
a	1980-1981			x	x x x	x x x	x x x	x x x	x x x	x x				Patton (1984)
	1981-1982			x	x x x	x x x	x x x	x x x	x x x	x x x				Ahl (1983)
B	1970-1971			--	--	--	x x x	x x x	x x x					Wolt (1972)
	1971-1972					x x x		x x x	x x x					Wolt (1972)
	1972-1973			x	x x x	x x x	x x x	x x x	x x x					Lanway (1974)
	1973-1974			x	x x x	x x x	x x x	x x x	--	--				Lanway (1974)
	1980-1981			x	x x x	x x x	x x x	x x x	x x x	x x				Ahl (1983)
	1981-1982		x	x	x x x	x x x	x x x	x x x	x x x	x x x				Ahl (1983)
C	1970-1971			--	--	--	x x x	x x x	x x x					Wolt (1972)
	1971-1972					x x x	x x x	x x x	x x x					Wolt (1972)
	1972-1973			x	x x x	x x x	x x x	x x x	x x x					Lanway (1974)
	1973-1974			x	x x x	x x x	x x x	x x x	--	--				Lanway (1974)
1	1970-1971			--	--	--	x x x	x x x	x x x	x x x				Wolt (1972)
	1971-1972					x		x x x	x x					Wolt (1972)
	1972-1973			x	x x x	x x x	x x x	x x x	x x x	x x x				Lanway (1974)
	1973-1974			x	x x x	x x x	x x x	x x x	--	--				Lanway (1974)
	1991-1992					x	x x x	x x x	x x x	x x x				Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x	x x x			Alexander +
14	1991-1992			x	x x x	x x x	x x x	x x x	x x x					Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
16	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
17	1991-1992			x	x x x	x x x	x x x	x x x	x x x	x x x				Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x	x x x			Alexander +
18	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
21	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
22	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
29	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
34	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
35	1988-1989			--	--	--	x x x	x x x	x x x	x x x				Gallagher
	1989-1990					x	x x x	x x x	x x x					Gallagher
	1990-1991						x	x	x x x	x x x				Gallagher
	1991-1992			x	x x x	x x x	x x x	x x x	x x x					Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
36	1988-1989			--	--	--	x x x	x x x	x x x	x x x				Gallagher
	1989-1990		x	x	x x x	x x x	x x x	x x x						Gallagher
	1990-1991						x	x	x x x	x x x				Gallagher
	1991-1992			x	x x x	x x x	x x x	x x x	x x x					Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
37	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
38	1991-1992			x	x x x	x x x	x x x	x x x						Syrdahl (1993)
	1994-1995			--	--	--	x x x	x x x	x x x	x x x				Alexander +
39	1991-1992					x	x x x	x x x	x x x					Syrdahl (1993)
41	1994-1995			--	--	--	x x x	x x x	x x x					Alexander +
42	1994-1995			--	--	--	x x x	x x x	x x x					Alexander +

+ Complete citation, Alexander and Schlising (1997).

General pool differences include the following. 1) Pools A and B, the only adjacent pools on a drainage channel, displayed different flooding times in the

four years they were both visited. The lower pool, B, had surface water up to one month earlier (Wolt, 1972). 2) Pool 34 received water directly from clay

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soils that drained Pool 35 with some delay in flooding. 3) Pool 36 flooded early in 1989-1990, and contained water much longer than adjacent pool 35. In contrast, the next year these pools both flooded late at the same time and Pool 35 held water longer than Pool 36 (Gallagher, 1992). 4) During low rainfall times of initial filling, the large basins of Pools 1 and 17 contained small independent pools that remained in Pool 1 throughout the 1971-1972 season (Wolt, 1972). 5) Pools 1 and 17 displayed a maximum depth only during a few years with high rainfall. At this time, Pool 17 was connected to Pool 16 (the only observed direct water connection between pools). 6) Pools in grazed watersheds flood earlier than comparable pools in ungrazed watersheds (Marty, 2005). This was supported by the observation of Pool 29 flooding weeks earlier than other pools in 1991-1992. There was grazing in this pool watershed, located north of Lassen Road, with no grazing in other pool watersheds on VPP (Syrdahl, 1993).

OBSERVATIONS ON VERNAL POOL INVERTEBRATES

The following sections, organized in a taxonomic sequence, consider specific vernal pool aquatic invertebrates independently selected by investigators. Brief comments have been added about a few taxonomic groups not studied in detail. This report does not provide a literature review of similar studies done in other temporary pool systems. Many vernal pool invertebrate species were not studied. Differences in flooding patterns discussed above, make it impossible to predict life history patterns and community composition as occurring on specific chronological dates.

The species considered represent a fraction of the aquatic invertebrate diversity in vernal pools. The taxonomic understanding of vernal pool invertebrates has never been strong (Simovich, 1998) and additional research is needed. Unfortunately, there is little financial support and commitment to promote the study of invertebrate taxonomy and ecology. This is particularly unfortunate because increasingly sophisticated molecular analyses along with world-wide electronic communication between specialists provides a unique opportunity to expand taxonomic and ecological information on temporary pool invertebrates.

Phylum Mollusca; class Gastropoda: *Fossaria (Bakerilymnaea) sonomensis* *Vernal pool snail*

This narrative was derived from my observations and Gallagher's study of the vernal pool snail from 1988 through drydown in 1991 (Gallagher, 1992, 1993). Snails were observed in Pool A in 1967-1968 (Michener, 1970). They were collected in all of the fourteen largest pools on VPP in 1992 (Syrdahl, 1993).

Vernal pool snails over-summer within pool sediments and are activated as these sediments become hydrated. Snails and snail egg masses were observed immediately after flooding. An initial drop in snail density was hypothesized to be due to mortality associated with high energy demands and a reduced availability of periphyton (a film of plants and animals attached to submerged objects). After pools were established, snail feeding tracks were observed in the established periphyton.

Snail embryonic development was observed through gelatinous membranes in eggs that were part of masses often attached to rocks. I observed a case-making larval caddisfly (sand grain case) feeding on snail egg masses in pool A in the late 1960's. These caddisfly larvae were not observed in VPP pools. One month was required for development of eggs to spat (small snails) in 1990 and 1991. Large numbers of spat break out of the egg mass as water temperatures increase above 10° C.

Snails require more than the remaining pool season before becoming reproductively active; as a result, pool condition the previous years influence snail size distribution. Larger (older) snails reproduce for several years and genetic diversity would be increased if different age snails exchange gametes.

During any one year, adjacent pools of different pool volumes (resulting in different water temperatures) contained snails with different growth rates and fecundities. Snails transferred by Gallagher from one pool to the other assumed growth characteristics of snails found in the pool to which they were relocated.

Snails entered the sediments before drydown with the larger (older) snails entering first. This is assumed to be a behavioral adaptation to avoid high temperatures. At this time, the snails are protected by the sediments and isolation provided by the shell

and a mucus coat (epigram) covering the aperture. Syrdahl (1993) only recorded snails absent during a late collection (27 May) before drydown. I observed large and small dead snails on surface sediments during one year, assumed to have experienced a rapid water temperature increase that killed snails before they could enter the sediments. Pools that held water for less than three months did not support snails. In the rare years when larger pools held water for less than three months, snails produced in previous years apparently maintained the population.

Newman (Newman, 1973; Newman and Thomas, 1975) placed field-collected snails in laboratory containers. As the water in these containers evaporated, the snails moved into sediments on the floor of the containers, that were mimicking field conditions. Examples of freshly collected snails and snails maintained in dry sediments in the laboratory for 30, 97 and 174 days were sampled for nitrogen levels. Reduced metabolic activity was indicated by a drop in total nitrogen levels after 30 days. A shift in nitrogen metabolism from ammonia nitrogen to urea and eventually to uric acid represented a physiological adaptation supporting summer survival with low water availability. Gallagher's observation that the smallest snails failed to survive aestivation in 1991 indicates a minimum size was required for successful aestivation.

Phylum Arthropoda
subphylum Crustacea

Class Branchiopoda; Order Cladocera—water fleas. Three morphotypes of water fleas were collected by Syrdahl in 1992 (Syrdahl, 1993). They were collected in various combinations including all three in one pool and all absent from another pool. In spring, some pools contained large populations of planktonic cladocera reproducing by parthenogenesis. At this time, diversity using the number of individuals was compromised because disturbance of individuals during collection caused the discharge of next generation individuals from female brood pouches (Alexander and Syrdahl, 1992). As ponds dried, individuals were observed carrying ephippia, the summer resistant stages.

Class Branchiopoda; Order Anostraca—fairy shrimp. Three species of fairy shrimp were observed.

1. *Branchinecta conservatio*, conservancy fairy shrimp. This species was collected in seven of the

fourteen larger pools on VPP in spring 1992 (Syrdahl, 1993). Soil collections from Pool 35 in July 1993, initially cooled and saturated before flooding with distilled water at 10°C, produced mature adults of this species in two months (Eads, 1995). The conservancy fairy shrimp was listed as endangered on 19 September 1994 (Federal Register, 1994).

The conservancy fairy shrimp was observed in eight of seventeen larger pools on VPP in spring 1995, with high population densities restricted to the four largest pools (Alexander and Schlising, 1997, 1998). In one of these large density populations (Pool 35), density estimates (number per unit volume sampled) of breeding adults were multiplied by the calculated pool size to determine the following population size estimates: 1) 300,000 on 16 March, 2) 100,000 on 13 April, and 3) 50,000 on 27 April. No individuals were collected during the following weeks. I estimate that the four high density populations totaled over two million breeding adults that year.

Six pools had low population densities ranging down to 0 (present in 1991 and not in 1995). The rate of development was rapid in smaller pools. The small populations observed in smaller pools could be attributed to a lower number of cysts in the sediments; however, that is unlikely, considering the large number of cysts produced per individual. It is likely that the conditions in these smaller pools, that have cysts in sediments, do not support viable populations every year because variation in environmental conditions influence cyst hatch and/or juvenile survival.

Although turbidity in larger pools may reduce the feeding effectiveness of visual predators on conservancy fairy shrimp, avian predators, tadpole shrimp and *Notonecta kirbyi* and *Berosus* (Syrdahl, 1993) were observed in large turbid pools.

Eads (1995) used RAPD (Random Amplified Polymorphic DNA) to compare *B. conservatio* adults collected in February/April 1994 from Olcott Lake in Jepson Prairie Preserve (Solano County) and at Pool 35 in VPP, landscapes separated by 190 km. The 27 markers used were positive in both populations. The measure of genetic diversity within populations (heterozygosity) was high in both populations. Marker frequency indicated individuals collected in the two pools represented separate populations and the genetic distance between these populations matched differences expected between races of the same species.

2. *Branchinecta lynchi*, vernal pool fairy shrimp.

During the 1991-1992 season, this species was collected from 17 February to 16 March in three shallow pools (maximum depth 14 cm) (Syrdahl, 1993). In mid February 1993, seven of 35 small pools (surface areas under 40 m²) contained vernal pool fairy shrimp that were absent from the same pools in late February and March (Marsters, unpublished undergraduate research). The vernal pool fairy shrimp was listed as a threatened species on 19 September 1994 (Federal Register, 1994). The failure to see this species in spring 1995 (Alexander and Schlising, 1997) was because collections started in March 1995 and emphasized larger pools.

During the 1992-1993 season in the Chico area, multiple hatches of vernal pool fairy shrimp were observed during cold water reflooding of shallow pools. These pools developed females with cysts in six weeks after December flooding and in three weeks after two spring refillings (Gallagher, 1996).

Rapid development to a large body size in small pools reduces invertebrate predation on the vernal pool fairy shrimp. At VPP, vernal pool fairy shrimp complete reproduction before tadpole shrimp reach a large size and before the number and diversity of insect predators increases. (Syrdahl observed the number of predatory insect taxa collected was low in February and March and almost tripled in April.) Furthermore, winter season predations of *Notonecta kirbyi* will unlikely impact all populations of vernal pool fairy shrimp in the numerous, vegetation-filled pools.

Although a cyst reserve will maintain populations in these scattered small pools, movement between pools would be needed to reestablish populations after disappearance. Birds feeding on mature females would potentially move cysts between pools. This is likely important because of the high avian activity earlier in the year (Bogiatto and Karnegis, 2007). Vernal pool fairy shrimp observed in pools formed along a disked fire break (Marsters, unpublished undergraduate student research) indicates a high dispersal rate.

3. *Lindieriella occidentalis*, California lindieriella.

From fall 1981 through spring of 1983 Patton (1984) observed a relatively uniform cohort of planktonic developmental stages starting one week after flooding. Females carrying cysts were observed in five weeks and individuals disappeared from the water in 20 to 23 weeks. In 1992, biweekly collections on

VPP found this species in nine intermediate size pools; however, it was absent from the two largest pools (Syrdahl, 1993). In spring 1993, this species was the only fairy shrimp in 6 of 35 small pools (surface areas from 60 to 590 m²) (Marsters, unpublished undergraduate student research). This species took eight weeks to mature and did not show additional hatching after pool refilling during 1992-1993 in the Chico area (Gallagher, 1996).

In 1995, California lindieriella on VPP had high densities, even in pools that had high densities of the conservancy fairy shrimp, and it was again absent from the two largest pools (Alexander and Schlising, 1997). It was the last species of fairy shrimp surviving (May, 1995), and was collected in pools with invertebrate predators.

General comments about fairy shrimp. In 1992, 13 of the 14 larger pools (93%) on VPP contained at least one species of fairy shrimp and 6 (43%) had two species, California lindieriella with the vernal pool fairy shrimp in one smaller pool and with the conservancy fairy shrimp in five larger pools (Syrdahl, 1993). During the 1992-1993 season in the Chico area, Gallagher (1996) statistically established that pools supporting vernal pool fairy shrimp were smaller and shallower (with shorter duration) than pools supporting California lindieriella (the conservancy fairy shrimp was not found in this area). The vernal pool fairy shrimp and California lindieriella were observed independently in 14 of 35 small pools with the vernal pool fairy shrimp only in smaller pools (Marsters, unpublished undergraduate student research). Collections on VPP starting in March 1995 found either California lindieriella or the conservancy fairy shrimp in all 17 pools examined, with both species observed in 5 pools (29%).

Eriksen and Belk (1999) list all three species as "swimming together." The VPP observations indicate that the two species of *Branchinecta* would rarely be found together, as the vernal pool fairy shrimp grows rapidly in small pool habitats that were dry when the conservancy fairy shrimp were reproductively active. This is similar to the relationship described by Hathaway and Simovich (1996) in the San Diego area where the Riverside fairy shrimp (*Streptocephalus woottoni*) is found in larger, longer-lasting pools and San Diego fairy shrimp (*Branchinecta sandiegonensis*) is found in the smaller pools. They felt differences in rate of development explained the pool separation and the same can be said of the two *Branchinecta* species on VPP.

Collections of large single size cohorts of the conservancy fairy shrimp and California linderiella indicate a single hatch occurred over a limited time, in contrast to the multiple hatches of the vernal pool fairy shrimp during one year (Gallagher, 1996). I did observe a rare second hatch of the conservancy fairy shrimp associated with a drought year pool drydown and winter reflooding (1991, Table 4). Cooler temperatures blocked fairy shrimp maturation. Preadult collections of conservancy fairy shrimp and California linderiella matured in laboratory aquaria weeks before reproduction was observed in the field.

These observations place the three species of fairy shrimp on VPP in a gradient of pool types, with the conservancy fairy shrimp the only species using the largest pools and found in intermediate size pools, California linderiella found in intermediate size pools and the vernal pool fairy shrimp the only species using smallest pools also found in larger, shallow pools. The large numbers of California linderiella in intermediate size pools could be a factor influencing the separation of the two species of *Branchinecta*. For unknown reasons, California linderiella was never collected in the largest pools although one of these pools had an infrequent surface water connection to a pool that contained California linderiella. Field testing, to determine the shifting importance of pool temperature, turbidity, competition and predation on distributional patterns of all three species is important but will be difficult to determine because of the annual and seasonal variability of these conditions.

Field surveys that examine dip nets in the air are killing fairy shrimp briefly stranded on net fibers before they are returned to the water (Kirn, 1997). This mortality factor would be most severe with vernal pool fairy shrimp, because the few individuals observed represent a high proportion of a small pool population. Collecting individuals funneled into a bottle behind a plankton net allowed examination of individuals in the water and reduced collection mortality (Alexander and Schlising, 1997).

Class Branchiopoda; Order Notostraca—tadpole shrimp, *Lepidurus packardii*, vernal pool tadpole shrimp. Unless cited, this narrative was derived from Ahl's field and laboratory work (Ahl, 1983, 1991) and Alexander's field observations (including Alexander, 1976; Alexander and Schlising, 1997, 1998). Michener (1970) recorded tadpole shrimp in Pool A in 1967-1968. Lanway (1974) observed

them in Pools A, B, C and 1 in 1972-1973. Ahl studied tadpole shrimp in Pools A, a and B from fall 1980 to spring 1982. Tadpole shrimp were collected in 11 of 14 largest pools (79%) on VPP in spring 1991 (Syrdahl, 1993). In the same area, they were observed in 2 of 35 small pools (6%) in spring 1993 (Marsters, unpublished undergraduate research). The vernal pool tadpole shrimp was listed as endangered on 19 September 1994 (Federal Register, 1994). In 1995, I observed them in 15 of 17 larger VPP pools (88%).

Dry tadpole shrimp cysts hatched at 10° C, but did not hatch at 20° C (Lanway 1974). Total time from wetting to a free living stage was 2 to 3 weeks. Cysts took up water, became sticky and expanded to a 0.5 mm ball. In a stage called prehatching, the sticky, orange outer coat cracked revealing a developing embryo through a transparent membrane. The metanauplius, observed through the membrane, rotated and expanded before it hatched and bumped along the sediments for less than two hours before molting into a neonatant larva. Neonatant larvae had adult morphology. The fall hatching of over-summering cysts was observed over several weeks. Individuals with carapace lengths of a few mm were collected in fine-mesh nets pulled along the pool floor weeks after flooding (early December 1980) and females started producing cysts at a carapace length of 10 mm (early January 1981).

Adult female tadpole shrimp deposit cysts in an enlarged 11th thoracic appendage. Cysts are discharged to the environment during and between molts. In order to determine maximum fecundity, pairs of male and female shrimp were isolated in the laboratory and observed daily. When cysts were observed, females were removed and placed in individual chambers on a mesh screen because tadpole shrimp consume cysts. The smallest reproductively active females were 10 mm in carapace length producing an average of 9 cysts and the largest (31 mm in carapace length) produced an estimated 10,000 cysts.

Annual second generation hatching from freshly deposited cysts was established by laboratory experiments and supported by field observations. In the laboratory, the second generation hatch was high at 10°C and significantly lower at higher temperatures with unhatched cysts becoming part of the cyst bank.

A significantly higher number of males hatched under warmer conditions in the second generation

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hatch in the spring of 1981 and in a hatch during an early October pool flooding in 1981.

In spring 1981, Ahl observed metacercariae of an echinostome fluke eliminated first generation fecundity by parasitic castration. Dr. R. S. Demaree, CSU, Chico helped Ahl identify the flukes and encouraged John Eads to look for flukes in vernal pool snails in 1993. No flukes were found (John Eads, personal communication). Two hypotheses explain the failure to find flukes in 1993. 1) Parasites were restricted to the pools sampled by Ahl (A, a and B) and not in the pool sampled by Eads (Pool 35). 2) Parasites observed by Ahl were a chance introduction from other aquatic environments. The first hypothesis is unlikely as the pools are only separated by a few km and I have observed ducks flying between these areas. The second hypothesis implies that flukes introduced by waterfowl were typically associated with different wetland hosts and are not necessarily introduced annually. If this is the case, the impacts of the fluke on tadpole shrimp fecundity and snail survival would occur only infrequently.

Oxygen stress, indicated by tadpole shrimp swimming upside-down on the surface, was observed in late April 1992 with viable individuals collected from the same pool in following weeks (Syrdahl, 1993). No oxygen stress was reported by Ahl in spring 1981 and spring 1982. On 18 May 1995, tadpole shrimp were normal in the morning, observed swimming upside-down on the surface in the early afternoon, and the total populations were dead on the surface of two pools by evening (Alexander and Schlising, 1997). These dead tadpole shrimp attracted birds that were actively feeding on them. The smallest dead on the surface were second generation individuals containing cysts, and many cyst-carrying females were observed. Although smaller pools were dry at this time, the remaining larger (cooler) pools did not display tadpole shrimp under oxygen stress until June.

Only the larger, long-lasting pools allow the development of numerous second generation individuals and the survival of a few large first generation individuals that deposit large numbers of cysts. These pools represent important cyst banks in the landscape. There is reduced fecundity in intermediate size pools due to mortality of second generation individuals by oxygen stress or parasitic castration. The smallest pools apparently contain tadpole shrimp that rarely produce cysts and I assume they are maintained by dispersal.

Class Branchiopoda; Order Spinicaudata (Conchostraca)—*Cyzicus californicus*, California clam shrimp. Information on the clam shrimp is incomplete, combining research by Wolt (1972) and Lanway (1974) with general collections made after a twenty year gap. The life history narrative was derived from studies by Wolt (1972). Individuals were observed after 18 December 1967 with first females carrying cysts observed on 25 March 1968 and dead adults lining the mud during drydown in April (Michener, 1970). In late March 1971, Wolt chose four pools with high clam shrimp densities (Pools A, B, C and 1), establishing a weekly collection program that extended through the 1971-1972 season. He used preserved collections available in my laboratory from Pool A to complete the 1971-1972 season and to project responses in other pools. Individuals were both preserved and returned to the laboratory for further study. Dried cysts, found in dead females stranded on the dry pool surface, were used for laboratory hatching experiments.

Clam shrimp cysts hatched without the low temperature treatment required by tadpole shrimp (Wolt, 1972; Lanway, 1974). Prehatching, as described with the tadpole shrimp, was observed with clam shrimp; however, six planktonic naupliar stages followed. These small individuals moved and fed in the water column and were attracted to light with the seventh stage moving away from light starting to assume adult morphology. In the sediments, leg activity, within a dorsally attached, bilobed carapace ("shell"), moves pool water into the animal and filters out food. Each molt is marked by the addition of a concentric growth ring to the carapace. Although these stages are often found in the soft pool sediments, they do swim, and adults in copulation are observed in the water column. Adults with cysts were observed after 6 weeks in 1972 and 16 weeks in 1971 (see below).

Wolt identified developmental stages, counted the number of growth rings, measured carapace size, sexed adults and counted the number of cysts carried by adult females in weekly collections. Three clam shrimp population responses were observed. 1) Clam shrimp grew slowly in cold winter pools that flooded early (November and December) and dried in April (all Pools in 1970-1971, and Pool C in 1971-1972). 2) Clam shrimp grew rapidly in warmer pools that flooded late (February) and dried in April (Pools A and B in 1971-1972). 3) Clam shrimp failed to complete reproduction in Pool 1 during 1971-1972. At drydown, clam shrimp with

cysts had similar body sizes; however, the numbers of growth rings were higher in fall-flooding pools compared to the February-flooding pools.

Reproductively active clam shrimp were observed in Pool 1 in 1972-1973, the year following reproductive failure (Lanway, 1974). This indicates a cyst reserve bridged the previous year's reproductive failure. In the early 1980's, I failed to observe clam shrimp during intensive collections from Pools 34, 35, 36 and 37 (these pools are similar to Pools A and B); unfortunately other pools were not surveyed. In 1991, seven quantitative collections in Pool 1 from 17 Feb to 11 May failed to find clam shrimp (Syrdahl, 1993). The absence of clam shrimp in Pool 1 was further supported by my failure to observe clam shrimp in nine quantitative collections from 4 April to 29 May in 1995 (Alexander and Schlising, 1997). Syrdahl failed to observe clam shrimp from any pool visited during her spring 1991 survey of 14 large pools on VPP. I observed clam shrimp at low densities in Pools 17 and 22 (pools visited by Syrdahl) during my spring 1995 survey of 15 pools on VPP.

The disappearance of clam shrimp from Pool 1, associated with an assumed landscape-wide clam shrimp loss, can be explained in a variety of ways—especially when considering rainfall patterns introduced earlier in this paper. Although Wolt was distressed at the time, it is fortunate that he observed reproductive failure in 1971-1972. The climate analysis indicates that conditions supported pool formation for clam shrimp two years following Lanway's observation of a viable population in 1972-1973. However, in 1975-1976, the total rainfall at Red Bluff was even less than the total recorded when Wolt observed reproductive failure. The next year (1976-1977) had rainfall totals within 10 mm of the 1971-1972 year, including 20% of the low total rainfall after May 9, resulting in two consecutive seasons where it is doubtful Pool 1 could support clam shrimp reproduction. This supports the idea that reproductive failure (caused by drought) occurred for two successive years, following the documented failure four years earlier (Wolt, 1972). If this explains the absence of clam shrimp, they have not successfully reinvaded the pool during the long time between observations. General observations indicate a landscape loss of clam shrimp with deeper pools (e.g., Pool 17) providing important refugia for clam shrimp that have not increased enough to repopulate pools by dispersal. Alternatively, the high populations of clam shrimp observed in the 1960's and 1970's could be more atypical

with populations more likely to be found in only a few pools.

A variety of interacting factors influence clam shrimp population dynamics. Because cysts were observed to hatch when flooded with warmer water, some hatching will produce unsuccessful cohorts when they hatch during late spring or early fall flooding that results in short duration pools. This reproductive failure is more likely in this species because it requires more than one month of appropriate aquatic conditions to develop cyst-producing adults. Late season cyst production, typical of this species, may reduce the chance for cysts to be mixed in pool sediments, reducing the chance that they will be retained for more than one year. Further observations and testing are needed to describe clam shrimp dispersal, cyst bank retention and factors necessary for cyst hatch and the production of adults on VPP.

General Comments about Large Branchiopods. Although the large body size may provide adaptive benefit by reducing invertebrate predation, all these species have free-living developmental stages. They display an impressive increase in size from freshly hatched microscopic larvae to reproductive adults—a process that must be completed before annual dry-down. The vernal pool wetting phase (Keeley and Zedler, 1998) provides important cues (e.g., cold pre-wetting) (Lanway, 1974) that aids rapid development after pool flooding.

The gradient of vernal pool types from short-lasting (generally small) to long-lasting (generally larger and deeper) vernal pools tends to sort out different branchiopod species although they have similar adaptations to temporary pools. The observed loss of clam shrimp and the proposed importance of refugia pools may portend future problems with fairy shrimp and tadpole shrimp.

Cysts connect populations in time and space by withstanding the hot and dry phase of the ecosystem and withstanding transit in bird digestive systems. Although many cysts hatch the next pool season, some remain unhatched for multiple years providing a bridge over drought years. This "cyst bank" potentially develops in a variety of ways: cysts deposited at the edge of the largest pools will be in reserve until this area is again flooded; cyst reserves will be increased when low oxygen levels (expected deeper in the sediments) block hatching (Lanway, 1974); additionally, if cysts of individual species require a range of temperature and water clues to hatch, the

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conditions of any year may result in some not hatching. Bogiatto and Karnegis (2007) have established waterfowl feeding on these invertebrates, and if cysts remain viable they are transported from pool to pool.

Class Ostracoda—seed shrimp. Michener (1970), observed “Ostracoda” in Pool A. Syrdahl (1993) identified five morphospecies by size and color (small green, small white, small purple-green, large light green, large white). Four of these were collected in all pools. Marsters (undergraduate student research) found all thirty-four smaller pools surveyed contained a small green ostracod.

Class Copepoda—copepods.

Order Harpacticoida. These small animals (Syrdahl reported a length of 0.5 mm) are found in the sediments of some vernal pools. Syrdahl (1993) collected harpacticoids in seven of the fourteen pools surveyed. Gallagher (unpublished student research) observed harpacticoids hatching in the laboratory when wetting dry season sediments.

Order Cyclopoida. Cyclopoids are often observed in shallow edges of winter vernal pools. Michener (1970) collected cyst-bearing adults within days after pool flooding (indicating an older diapause stage over-summered) and observed them throughout the 1967-1968 season. Syrdahl (1993) reported cyclopoids in all pools in February and March and in no pools after late April.

Order Calanoida. Two calanoid copepods, *Leptodiaptomus tyrrelli* and *Hesperodiaptomus eiseni* are abundant vernal pool zooplankton. Many (but not all) individuals of the smaller species, *Leptodiaptomus tyrrelli*, pass through the standard mesh of common dip nets. Michener (1970) studied both species in Pool A during the 1967-1968 season. Ballantyne (1994) studied *Hesperodiaptomus eiseni* from 1990 through 1993 on VPP. Syrdahl (1993) collected both species in all pools surveyed. Marsters (unpublished undergraduate student research) observed calanoid copepods (no species identification) in all thirty-four smaller pools surveyed.

Weekly pool collections were used by Michener to describe life history patterns of both species in 1967-1968. Both hatched in different early developmental stages in December 1967—*L. tyrrelli* early nauplii (stage 1) and *H. eiseni* older nauplii (stage 4). Although both species grew at a similar rate, the hatch of more advanced nauplii resulted in copepodids and

adults of *H. eiseni* produced weeks earlier (12 February) than *L. tyrrelli* (4 March). At the time *L. tyrrelli* adults were observed, the youngest developmental stages were late stage copepodids. Two weeks following the production of cysts, nauplii representing a second generation of *L. tyrrelli* were collected. The second generation developed rapidly producing smaller adults. *Hesperodiaptomus eiseni* did not have a second generation.

Ballantyne (1994), was interested in feeding of copepods and field-fixed *H. eiseni* for electron microscopy and collected living individuals for laboratory study. Ectoparasitic microbes were attached to all parts of the body with reduced presence in the feeding currents that had smooth integument. Laboratory observations established that microorganisms were removed from the water, accumulating in feeding currents containing mucus-like strands produced at the base of the swimming legs. Microorganisms (typical diameter of 0.4 to 1.4 micrometers—some as large as 3.0 micrometers) in the feeding current were also observed in the foregut. Hind gut observations indicated a loss of bacteria and surface wall perforation of larger cells. These observations point to the importance of the detritus food chain for filter feeding crustaceans.

Phylum Arthropoda *subphylum Chelicerata*

Class Arachnida, Subclass Acari—water mites. The vernal pool water mites were collected by Syrdahl in three pools in 1992 (Syrdahl, 1993). Water mites, parasitic on insects, were observed on corixids and would be expected in all pools.

Phylum Arthropoda *superclass Hexapoda*

Most vernal pool insects fly into pools as adults, producing aquatic larvae. The dry season location of invading vernal pool aquatic insects was not studied; however, insect invasion must be influenced by the presence of adjacent aquatic environments, and unpredictable storms and air temperatures impacting flight activity. Larval insects are often observed killed during pool drydown; however, winter invading insects are more likely to complete development. Some larval insects found regularly in the pools never complete development.

With the exception of a field study on *Notonecta kirbyi* predation (Kirn, 1997) and community collec-

tions (Syrdahl, 1993), the papers reviewed did not consider insects. The biweekly collections by Syrdahl and my field observations supply general taxonomic identification and some life history information. Collections made over many years are needed to determine if individual species are annually present. Unless noted, the references to insects are from Syrdahl (1993).

Order Ephemeroptera—mayflies. Larval *Baetis* were collected in late March and April in five pools on one date and one pool two times.

Order Odonata—dragonflies and damselflies. Larvae of *Erythemis* were observed in four pools within a few weeks or days before drydown. Three additional and different larval Odonata were found in different pools at one time during the month of drydown (April). No larval dragonflies were collected from two pools where ovipositing dragonflies were previously observed by Syrdahl. I assume most, if not all, of the dragonfly larvae failed to complete development.

Order Trichoptera—caddisflies. I observed sand grain case-making caddisfly larvae feeding on the vernal pool snail (*Fossarias sonomensis*) egg masses in Pool A in the late 1960s. No caddisflies were collected in VPP in 1992 by Syrdahl.

Order Heteroptera—aquatic bugs. Corixids are always found in the pools and, although adults are collected initially, nymphal stages are collected soon after flooding. Adult notonectids are common in the pools at low densities. Although nymphs of both groups were observed killed during drydown, sequential collections indicate corixids regularly complete development and notonectids rarely complete development.

In spring 1995, field enclosures were used to observe *Notonecta kirbyi* predation on fairy shrimp and larval corixids (Kim, 1997). *Lindleriella occidentalis* was used to represent fairy shrimp in the field experiments because the other species were federally listed. *Notonecta kirbyi* were observed predators on *L. occidentalis* and undoubtedly also feed on the other fairy shrimp. An unexpected mortality of fairy shrimp that were rapidly transferred by dip net to field enclosures compromised statistical analysis. In similar experiments, nymphal corixids experienced zero mortality during transfer and predation by *N. kirbyi* was established and found to be influenced by water temperature.

The corixid success is potentially due to their feeding on small animals, such as protozoans that are part of the detritus food chain. As a result, notonectids feeding on corixids also benefit from detritus energy. Although notonectids do not regularly complete reproduction in vernal pools, they are important predators in all vernal pools from initial flooding to final stages. Notonectids detect prey in a variety of ways not restricted to vision (Kim, 1997). As a result, conservancy fairy shrimp in highly turbid pools would be subjected to notonectid predation.

Order Coleoptera—aquatic beetles. Syrdahl (1993) collected aquatic beetles of four families:

1. Curculionidae—weevils. Syrdahl (1993) collected various stages of *Notiodes aeratus* in 10 pools. In 1995, I observed adult weevils feeding by cutting round holes out of the floating leaves of *Marsilea vestita* in shallow water during drydown. Beetles were observed backing down into the water on *M. vestita* petioles. The eggs or larvae must survive the summer in the plant tissue. Schlising (2007) observed *M. vestita* in many pools and I observed round holes left by the weevil in *M. vestita* leaves in several pools.

2. Haliplidae—crawling water beetles. This family was represented by one taxon identified as *Haliphus*. Syrdahl found these in single collections in April from three pools. I assume these herbivores were feeding on emergent vegetation.

3. Dytiscidae—predaceous diving beetles. Syrdahl found the following taxa (identified by genera) in the number of pools indicated (out of 14 pools sampled biweekly): *Agabus*, 12; *Oreodytes*, 12; *Deronectes*, 10; *Hydroporus*, 9; *Liodessus*, 8; *Coptotomus*, 2; *Hydrovatus*, 2; and *Laccophilus*, 1. A high probability of occurrence was indicated for *Hydroporus* found in every collection made in three pools and for *Liodessus* found in every collection made in one pool.

4. Hydrophilidae—water scavenger beetles. Syrdahl found the following taxa (identified by genera) in the number of pools indicated (out of 14 pools sampled biweekly): *Tropisternus*, 12; *Berosus*, 12; *Helophorus*, 11; *Hydrophilus*, 3; *Hydrochus*, 2; and *Cymbiodyta*, 2. *Helophorus* was found in every collection made in three pools. The water scavenger beetles are also considered predators (Thorp and Covich, 1991).

General comments about beetles. Adult beetles were collected at low densities and larval beetles were more abundant. With the exception of Curcu-

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lionidae, pupae were not collected. It was not determined how many of the spring 1992 beetle collections represent individuals that could have completed development. Beetles that arrive in the late spring must develop rapidly to take advantage of the rapidly disappearing aquatic environment. I assume that numerous dytiscid beetles (often two sizes) observed on surface mud during drydown developed in the pools. Regardless of reproductive success, adult beetles and the larvae they produce are significant predators in vernal pools. Larval beetles were regularly observed as predators in live collections and many organisms were consumed in transport to the laboratory if larval beetle predators were not removed.

Order Diptera—midges and mosquitoes. Syrdahl collected midge larvae in all fourteen pools. Gallagher (unpublished student research) observed midge larvae developing in laboratory-flooded dry sediment collections. The midge larvae were observed in an area without adult flies and represented hatching of a stage that resisted desiccation. I observed several generations during any one season with population numbers expanding as individuals bred in a variety of wetlands including pools formed by cattle hoof prints.

Syrdahl reported larval mosquitoes present in six collections. They were observed in four pools only once and three were in pools that were dry before the next collection. These infrequent observations imply that few if any individuals completed development. I have observed mosquitoes in pools caused by late rain reflooding of previously dry pools with larvae and pupae often found dead in the drying mud. Syrdahl did not observe pool reflooding during spring 1992.

INVERTEBRATE ADAPTATIONS TO VERNAL POOLS

Vernal pool invertebrates initiate growth rapidly, typically completing growth or critical life cycle stages before pool drydown. A variety of invertebrate strategies support survival during the dry summer. Snails move into the sediments, sealing themselves in their shells in a reduced metabolic condition. Large branchiopod crustaceans and calanoid copepods produce a diapausing embryo in an exoskeleton ball (cyst) that resists desiccation. Two insects were observed to withstand the dry summer, a midge that over-summers in a diapause stage and a weevil that summers as a parasite in a widespread

wetland plant (*Marsilea*). Many vernal pool insects invade the pools as adults that produce annually important aquatic developmental stages that are potentially killed at drydown. Early insect invaders (fall and winter) and those that have rapid development are more likely to produce adults before drydown.

Detritus energy is important in the newly forming winter pools and continues to be important in turbid pools. Bacteria, protozoa and the small invertebrates in the detritus food chain are important food of early developmental stages of crustaceans and young corixids. The detritus food chain is dependent upon organic material in the sediments from the previous year, connecting winter invertebrates with spring and summer plant production (Alexander and Schlisling, 1997).

The larger size of some branchiopods may be an adaptive benefit reducing invertebrate predation. Tadpole shrimp and the young of invading insects (some not completing development) are benthic predators that cannot be avoided when pools become shallow. Regardless of size and trophic relationships, all invertebrates are prey to birds.

MOVEMENT OF INVERTEBRATES BETWEEN VERNAL POOLS

Invertebrate dispersal by vertebrates must be important as a small number of pools have surface water connections. Water birds are often observed in the area flying between pools and it is assumed they move invertebrates and cysts from pool to pool. Coyotes, cattle and investigators could move individuals or cysts in the thick mud that accumulates on anything that walks through the pools.

Invertebrate behavior and life history are assumed to influence dispersal. Tadpole shrimp and conservancy fairy shrimp were moved into pools that did not annually support development to adults. Conservancy fairy shrimp separated by hundreds of kilometers had populations connected by dispersal (Eads, 1995). The local dispersal of vernal pool fairy shrimp was supported by the observation of populations in pools formed as a result of the disking of a fire break (Marsters, unpublished undergraduate student research). It would be interesting to use DNA analysis to rank the rate of dispersal of several different vernal pool invertebrates in a single landscape.

VERNAL POOL
INVERTEBRATE DIVERSITY

Invertebrate community diversity is difficult to measure using indices that include numbers of individuals (Alexander and Syrdahl, 1992). Developmental stages and adults of vernal pool invertebrates have different community relationships and major size differences that make it impossible to obtain representative numbers with single collection methods. Furthermore, inactive cysts in sediments should be included in diversity analyses. The greatest diversity of living macroinvertebrates in Vina Plains vernal pools was in intermediate size pools. Landscape analysis is required to observe all of the select invertebrates considered in this paper (similar to crustacean diversity considered by Simovich, 1998).

VERNAL POOL MANAGEMENT

California Central Valley vernal pool landscapes have experienced major changes due to habitat fragmentation and loss over the last two hundred years. Large numbers of invertebrates in California vernal pools (hundreds of thousands to millions) does not insure their survival when vernal pool landscapes are destroyed. There remain few if any intact vernal pool landscapes associated with piedmont benches around the edge of California's Central Valley. The vernal pool landscapes that remain, such as Vina Plains, are critically important if we hope to preserve vernal pools. Management requires a dynamic approach that adjusts to changing conditions (Alexander, 1987). It is unwise for management to attempt to construct vernal pools because biodiversity is difficult if not impossible to create (Kistner, et al., 1995). Furthermore, the top predator notonectids, found at low densities in individual pools, are influenced by the number of vernal pools in one landscape.

Management of vernal pool landscapes must consider the hot dry summer and cool wet winter as a single system (Alexander and Schlising, 1997). Preserved vernal pool landscapes must be large and diverse enough to contain different pools that support invertebrate populations under a run of extremely dry or extremely wet years. Preservation of natural vernal pool landscapes supports invertebrate dispersal allowing individual pools to have naturally changing community compositions. Long-term preservation will depend upon genetic exchange between different valley preserves (Alexander and Gallagher, 1995). Unfortunately, we can only estimate

the frequency of linkage between these areas prior to the expansion of human development.

Vernal pool landscape conservation efforts include solitary bees because of their importance as vernal pool plant pollinators. These bees are diapausing in ground brood cells during the aquatic phase of the pool and although most brood cells are in upland sediments those constructed in pool sediments (Thorp, 2007) must survive pool floor disturbance.

Natural preserves are now being modified by climate changes that will cause unpredictable changes in vernal pools. Understanding the impact of these changes will be difficult if not impossible without the preservation of complex vernal pool landscapes.

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LITERATURE CITED

- AHL, J. S. 1983. The Reproductive Biology and the Availability of Eggs to over Summer in the Tadpole Shrimp, *Lepidurus packardii*. M. A. Thesis in Biology, California State University, Chico, CA.

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- AHL, J. S. 1991. Factors affecting contributions of the tadpole shrimp, *Lepidurus packardii*, to its overwintering egg reserves. *Hydrobiologia* 212:137-143.
- ALEXANDER, D. G. 1976. Ecological aspects of the temporary annual pool fauna. Pages 32-36 in S. K. Jain (Editor), *Vernal pools: Their Ecology and Conservation*. Institute of Ecology, Special Publication 9. University of California, Davis, CA.
- ALEXANDER, D. G. 1987. Dynamic Master Plan for Vina Plains Preserve. Prepared for The Nature Conservancy. [This initial management plan was prepared with the help of Dr. Tom Griggs and the Vina Plains Management Committee.]
- ALEXANDER, D. G. and S. P. GALLAGHER. 1995. A proposal to form a committee to identify and coordinate vernal pool preserves and to oversee vernal pool mitigation in California's Central Valley. *Anostracan News* 3:1-2.
- ALEXANDER, D. G. and R. A. SCHLISING. 1997. Vernal pool ecology and vernal pool landscape management as illustrated by rare macroinvertebrates and vascular plants at Vina Plains Preserve, Tehama County, California. Report submitted to the California Department of Fish and Game. Region 1, Redding, CA.
- ALEXANDER, D. G. and R. A. SCHLISING. 1998. Patterns in time and space for rare macroinvertebrates and vascular plants in vernal pool ecosystems at the Vina Plains Preserve, and implications for pool landscape management. Pages 161-168 in C. W. Witham, E. T. Bauder, D. Belk, W. R. Ferren, Jr. and R. Ornduff (Editors). *Ecology, Conservation and Management of Vernal Pool Ecosystem - Proceedings from a 1996 Conference*. California Native Plant Society, Sacramento, CA.
- ALEXANDER, D. G. and R. SYRDAHL. 1992. Invertebrate biodiversity in vernal pools. *The Northwest Environmental Journal* 8:162-163.
- BALLANTYNE, R. J. 1994. Feeding Dynamics of *Hesperodiaptomus eiseni* from California Vernal Pools. M. S. Thesis in Biology. California State University, Chico, CA.
- BOGIATTO, R. J. and J. D. KARNEGIS. 2007. The use of eastern Sacramento valley vernal pools by ducks. Pages 111-118 in R. A. Schlising and D. G. Alexander (Editors), *Vernal Pool Landscapes*. Studies from the Herbarium, Number 14. California State University, Chico, CA.
- EADS, J. A. 1995. A Genetic Comparison of Two Populations of the Endangered Fairy Shrimp, *Branchinecta conservatio*, Using RAPD Techniques. M. S. Thesis in Biology, California State University, Chico, CA.
- ENG, L. L., D. BELK, and C. H. ERIKSEN. 1990. California Anostraca: distribution, habitat, and status. *Journal of Crustacean Biology* 10:247-277.
- ERIKSEN, C. H. and D. BELK. 1999. *Fairy Shrimps of California's Puddles, Pools and Playas*. Mad River Press, Eureka, CA.
- FEDERAL REGISTER. 1994. Endangered and threatened plants; determination of endangered status for the conservancy fairy shrimp, longhorn fairy shrimp and the vernal pool tadpole shrimp; and threatened status for the vernal pool fairy shrimp. *Federal Register* 59:48136-48153.
- GALLAGHER, S. P. 1992. Interpopulation Variation and the Life History of the Vernal Pool Snail, *Fossaria (Bakerilymnaea) sonomensis* in two Pools in Tehama County California. M. S. Thesis in Biology, California State University, Chico, CA.
- GALLAGHER, S. P. 1993. Life history variation in the temporary pool snail, *Fossaria sonomaensis*, in the Northern Sacramento Valley. *American Midland Naturalist*.
- GALLAGHER, S. P. 1996. Seasonal occurrence of habitat characteristics of some vernal pool Branchiopoda in Northern California. *Journal of Crustacean Biology* 16:323-329.
- HATHAWAY, S. A. and M. A. SIMOVICH. 1996. Some factors affecting the distribution and co-occurrence of two Southern California anostracans (Branchiopoda): *Branchinecta sandiegonensis* and *Streptocephalus woottoni*. *Journal of Crustacean Biology* 16:669-677.
- KEELEY, J. R. and P. H. ZEDLER. 1998. Characterization and global distribution of vernal pools. Pages 1-14 in C. W. Witham, E. T. Bauder, D. Belk, W. R. Ferren, Jr. and R. Ornduff (Editors). *Ecology, Conservation, and Management of Vernal Pool Ecosystems - Proceedings from a 1996 Conference*. California Native Plant Society, Sacramento, CA.
- KING, G. 1992. Geomorphology of piedmont vernal pool basins, California. *The California Geographer* 32:19-38.
- KIRN, S. A. 1997. Environmental Factors Affecting *Notonecta kirbyi* (Hemiptera: Notonectidae) Predation in Vernal Pools at Vina Plains Preserve, Tehama County, California. M. S. Thesis in Biology, California State University, Chico, CA.
- KISTNER, D. H., D. G. ALEXANDER and H. R. JACOBSON. 1995. Vernal Pool Creation and Restoration in California: A Study Plan for Evaluating Attainable Quality and Functional Performance. EPA/600/R-95/073. U. S. Environmental Protection Agency. Western Division, National Health and Environmental Effects Laboratory, Corvallis, OR.
- LANWAY, C. S. 1974. Environmental Factors Affecting Crustacean Hatching in Five Temporary Ponds. M. A. Thesis in Biology. California State University, Chico, CA.
- MARTY, J. T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology* 19:1626-1635.
- MICHENER, E. A. 1970. Population Dynamics of Two Species of *Diaptomus* (Copepoda: Calanoida) in an Ephemeral Pond. M. A. Thesis in Biology, Chico State College, CA.
- NEWMAN, K. C. 1973. Ammonia, Urea and Uric Acid Levels in Active and Estivating Snails, *Bakerilymnaea cockerelli*. M. A. Thesis in Biology, Chico State University, CA.

- NEWMAN, K. C. and R. E. THOMAS. 1975. Ammonia, urea and uric acid levels in active and estivating snails, *Bakerilymnaea cockerelli*. Comparative Biochemistry and physiology A. 50(1A):109-112.
- PATTON, S. 1984. The Life History Patterns and the Distribution of Two Anostraca, *Lindieriella occidentalis* and *Branchinecta* sp. [*Branchinecta conservatio*]. M. A. Thesis in Biology. California State University, Chico, CA.
- SCHLISING, R. A. 2007. The nature of summer plant life in large vernal pool basins at the Vina Plains Preserve. Pages 59-88 in R. A. Schlising and D. G. Alexander (Editors), Vernal Pool Landscapes. Studies from the Herbarium, Number 14. California State University, Chico, CA.
- SIMOVICH, M. A. 1998. Crustacean biodiversity and endemism in California's ephemeral wetlands. Pages 107-118 in C. W. Witham, E. T. Bauder, D. Belk, W. R. Ferren, Jr. and R. Ornduff (Editors), Ecology, Conservation, and Management of Vernal Pool Ecosystems - Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA.
- SYRDAHL, R. L. 1993. Distribution Patterns of Some Key Macroinvertebrates in a Series of Vernal Pools at Vina Plains Preserve, Tehama County. M. S. Thesis in Biology, California State University, Chico, CA.
- THORP, R. 2007. Biology of specialist bees and conservation of showy vernal pool flowers. Pages 51-57 in R. A. Schlising and D. G. Alexander (Editors), Vernal Pool Landscapes. Studies from the Herbarium Number 14. California State University, Chico, CA.
- THORP, J. H. and A. P. COVICH. 1991. Ecology and Classification of North American Freshwater Invertebrates. Academic Press, San Diego, CA.
- UNIVERSITY OF CALIFORNIA STATEWIDE IPM PROGRAM. 2006. California Weather Data. <http://www.ipm.ucdavis.edu/WEATHER/wxretrieve.html> (accessed May 2006).
- WOLT, T. B. 1972. *Cyzicus mexicanus* (Crustacea: Conchostraca) Life History and a Comparison of Growth, Maturity and Egg Production in Five Ponds. M. A. Thesis in Biology, California State University, Chico, CA.