

Odonate exuviae used for roosts and nests by *Sassacus vitis* and other jumping spiders (Araneae: Salticidae)

Tim Manolis¹

¹ 808 El Encino Way, Sacramento, CA 95864, USA, email: Ylightfoot@aol.com

Abstract: I systematically collected dragonfly (Anisoptera) exuviae along the margins of backwater lagoons in the American River floodplain, Sacramento County, California, USA, in five years (2008-2010, 2012-13) to document and monitor secondary use of these structures by arthropods, particularly spiders. Of nearly 400 exuviae examined, 28.1% were occupied, or showed signs of occupancy (*e.g.*, unoccupied retreats). Of these occupied exuviae, 93% contained spiders or evidence of spider occupancy, and at least 50% of these were occupied by *Sassacus vitis* (many unoccupied retreats were probably of that species as well). *S. vitis* showed a significant preference for using the exuviae of sedentary, burrowing dragonfly larvae versus those of active, clasping or sprawling larvae. I found *S. vitis* in exuviae as single males and females, in pairs, and using exuviae for molt retreats and nests. Thirty-four *S. vitis* nests in exuviae provided data on aspects of the species' breeding biology. In addition, a number of these nests were attacked by hymenopteran egg parasitoids in the genera *Idris* (Platygastridae) and *Gelis* (Ichneumonidae). I also found three other salticid species (*Sitticus palustris*, *Synageles occidentalis*, and *Peckhamia* sp.) in exuviae, all guarding egg sacs. Utilization of dragonfly exuviae by *Sassacus vitis* and other salticids is no doubt more frequent and widespread than previously noticed and deserves further scrutiny.

Key words: *Sassacus vitis*, Salticidae, dragonfly exuviae, retreats, breeding biology, egg parasitoids

Introduction

Jumping spiders (Salticidae) actively stalk their prey and most do not build prey-capture webs, but they do use silk to weave retreats for roosting, molting, mating, and nesting. These retreats are typically placed in various more-or-less protected locations reflecting the wide variety of habitats occupied by these spiders, including: in vegetation (*e.g.*, curled leaves, inflorescences), under tree bark, in crevices in trees, fences and walls, or under surface objects on the ground (Jackson 1979; Edwards 1990; Richman & Jackson 1992; Jennings *et al.* 2008). Retreats have been documented occasionally in a number of other sites, for example, in insect galls (Miller 1966; Judd 1967), empty wasp nests (Araujo & De Maria 2008), retreats of other spiders (Boulton & Polis 2002; Johnson 1995), snail shells (Mikulska 1961), and dragonfly (Anisoptera) exuviae (Torralba-Burrial *et al.* 2007; Manolis 2008, 2013).

Dragonfly exuviae accumulate along the margins of nearly all bodies of fresh water, from the smallest pools and rivulets to large rivers and lakes. They may survive intact for anywhere from a few hours to a few months, depending on the degree to which they are sheltered from severe weather (wind and precipitation) and flooding. In many situations where the substrate is relatively uncomplicated – barren shorelines, stands of a few species of smooth-stemmed rushes, grasses and sedges – they add a significant element of structural complexity which can be exploited by arthropods in search of shelter and nest sites. It is not surprising, then, to read or hear anecdotal accounts of the occurrence of a wide range of arthropods, primarily spiders, using exuviae for shelters (Tyrrell 2004; Hutchinson & Ménard 2013; F. SaintOurs, pers. comm.). This phenomenon appears, however, not to have been previously subject to

intensive, systematic analysis. Most people who collect large series of dragonfly exuviae are, of course, odonatologists who are only marginally, if at all, concerned with the “squatters” they may encounter. Unless they collect large series at a few sites over a number of years and carefully document all arthropod inhabitants, they may not notice particular patterns of occupancy. Published accounts of any such patterns are few (Tyrrell 2004; Jäckel & Koch 2015). I here document the nature and extent of use of dragonfly exuviae for retreats by jumping spiders and other arthropods in riparian vegetation along the American River in the Central Valley of California. One species of jumping spider, *Sassacus vitis* (Cockerell 1894) (Figure 1), proved to be the dominant occupant of these exuviae; hence my primary focus is on this species’ occupancy patterns and aspects of its breeding biology, including the parasitism of its nests by various wasps (Hymenoptera).



Figure 1. Female *Sassacus vitis* found in a dragonfly exuvia along the shoreline of a backwater lagoon in the American River Parkway, Sacramento County, California on 24 May 2008. Photograph © Ray Bruun, used with permission.

Study area

I observed and collected odonate exuviae and spiders along the shoreline of the American River and backwater lagoons in the river floodplain, confined by levees, between river mile 11 and 12, adjacent to Rio Americano High School, Sacramento County (Figure 2; 38.5759° N, 121.3574° W). These shallow backwaters are usually connected to the river by narrow channels, but are for the most part separated from the deeper main river channel by a number of islands and peninsulas. Shoreline vegetation at the site is dominated by a variety of graminoid plants and forbs (*Juncus effusus*, *Schoenoplectus acutus*, *Iris pseudacorus*, *Sagittaria sanfordii*, *Artemisia douglasiana*, *Carex* sp., *Cyperus* sp., *Eleocharus* sp., *Ludwegia* sp., and *Polygonum* sp.). Areas of slightly higher ground are covered with dense thickets of horsetail (*Equisetum* sp.), blackberry (*Rubus* sp.), poison hemlock (*Conium maculatum*) and willows (*Salix* sp.), as well as trees including box-elder (*Acer negundo*), white alder (*Alnus rhombifolia*), oaks (*Quercus* spp.) and Fremont cottonwood (*Populus fremontii*). Most of the substrate of the lagoons is mud, but there is some sand and river gravel, particularly along the main channel and the small channels connecting the main channel to the lagoons.



Figure 2. Backwater lagoons in the floodplain of the American River, Sacramento County, California. Odonate exuviae were collected in emergent and shoreline vegetation around these lagoons.

When water levels rise, typically in the winter or mid-summer, these backwater lagoons are flooded, and are essentially subsumed within the expanded river channel when water levels approach flood stage. At very low river stages the lagoons may dry up sufficiently that some of them become isolated ponds, and extensive patches of emergent vegetation are then exposed above the water line on drying mudflats (Figure 3). Except at flood stages, the current is slow through this series of lagoons, resulting in thick beds of submerged vegetation and floating mats of algae and duckweed (*Lemna* sp).



Figure 3. Backwater lagoon in the floodplain of the American River, Sacramento County, California. Arrows indicate the extent of a drop in water level (the pale basal band on stands of *Juncus*). Such decreases (as well as increases) in water levels can happen over a few days or weeks as a result of manipulation of water flows at upstream dams.

River stages along the lower American River are strongly affected by releases from upstream dams (Nimbus and Folsom). The schedule of timing and extent of these releases is, in turn, affected by a number of factors, including the timing and extent of annual rainfall, snowmelt, water levels in upstream reservoirs, and the release of water for downstream users. These factors vary from year to year, creating significant annual variation in the timing and extent of high and low stages (Figure 4).

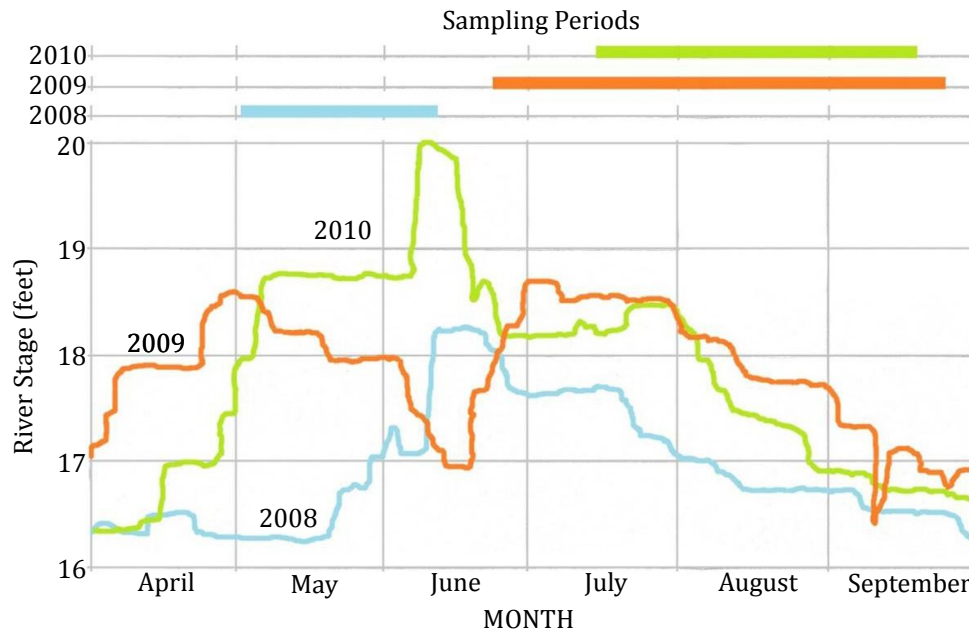


Figure 4. River stages and periods when exuviae were collected for three years of this study: 2008 (blue), 2009 (orange), and 2010 (green). River stage data were collected at the nearest monitoring station of the California Department of Water Resources, 4 miles downstream from the study site.

Methods

I made visual searches along the margins of the lagoons and river channel at this site on 22 dates in the following periods: 2 May – 10 June 2008 (4 dates), 22 June – 25 September 2009 (7 dates), 13 July – 16 September 2010 (7 dates), 6 July and 1 August 2012, and 22 May and 12 June 2013. Year-to-year differences in the timing of visits were primarily due to variation in the timing and extent of changes in water levels (Figure 4), particularly as this affected the peaks of odonate emergence and limited my access to areas of emergence. Searches for exuviae in late winter and early spring before flying odonates were first observed failed to detect any exuviae, suggesting that few if any exuviae survive flooding and severe winter weather from one year to the next.

A day's sampling effort was limited to about an hour's slow walk along the water's edge searching for exuviae. I waited at least two weeks, typically longer, before resampling the same stretch of shoreline, in order to provide time for new exuviae to accumulate and be visited by potential occupants. I examined all dragonfly (Anisoptera) exuviae of three families (Aeshnidae, Gomphidae and Libellulidae) of a size sufficient to house the silk retreats of small spiders. All such exuviae encountered were either opened in the field or collected for further study. Sampling times ranged from between 10:00 to 16:00 PDT. The number of exuviae collected or examined per visit ranged from 2 to 40 (mean = 17.74, SD = 8.35). Exuviae which were translucent enough to determine the absence of occupants or evidence of occupancy (*e.g.*, silk retreats) or which were inadvertently opened during collecting (*e.g.*, because they broke into

pieces while being extracted from vegetation) were included in the sample tally but discarded and not retained. The majority of the exuviae found were placed in plastic vials, usually one exuvia per vial except in rare instances when two or more exuviae were closely interlinked, usually by the legs, and attempting to separate them in the field risked damaging them. Exuviae were kept in these vials and checked regularly for signs of occupants. After a period of time, typically more than 40 days, by the end of which occupants were likely to have emerged, dormant exuviae were opened and examined for signs of prior occupancy.

Salticid nests were occasionally found to be attacked by wasps in the genus *Idris* (Platygastridae: Scelioninae) (identifications courtesy of L. Masner) and, in one instance, by a wasp in the genus *Gelis* (Ichneumonidae) (identification courtesy of R. Zuparko). *Idris* wasps are very small primary egg parasitoids. Females lay a single egg in each spider egg attacked, the larval wasp consuming the contents and emerging directly from the egg as a mature adult (Howard 1890; Eason *et al.* 1967). *Gelis* wasps lay one to a few eggs within spider egg sacs and the larvae devour eggs, pupate, and then emerge as adults from the egg sac (Fitton *et al.* 1987). Exuviae from which occupants, either spiders or wasps, emerged were monitored until the occupants died, at which time the exuviae were opened and any nests found were gently pried open and examined for signs of dead spiders or wasps, egg cases, infertile eggs or failed emergences, etc. The exuviae and all contents were then placed in 70% isopropyl alcohol in glass vials.

Some unoccupied exuviae collected of those species most frequently used for spider roosts were measured with dial calipers to determine the space available to the spiders. Spider retreats were restricted to the abdominal cavities of exuviae, so measurements were made of abdomen length (segments 1-9) and width (at the widest point, typically segment 6). Width measurements were reduced by 0.5 mm to account for the thickness of the abdominal wall. Sample sizes for measurement were 15 each for *Libellula luctuosa* Burmeister 1839 and *Tramea lacerata* Hagen 1861, the two most frequently collected and occupied exuvial types. Fewer exuviae suitable for measurement were available for less common species, so sample sizes were restricted to six for *Anax junius* (Drury 1773) and to three for *Plathemis lydia* (Drury 1773). The three dimensional shape of the abdominal cavity of most odonate exuviae, as well as that of many salticid roost and nest retreats, including those of *Sassacus vitis*, is approximately that of a tri-axial ellipsoid. My measurement of length and width correspond to measurement of the major and median axes, respectively, of such an ellipsoid. These measurements allow comparison with similar measurements of length and width of nest retreats collected for a variety of spider species by Vetter and Carroll (2013), in particular, nest retreats of *S. vitis*, *Phidippus audax* (Hentz 1845), and *Cheiracanthium* [either *C. inclusum* (Hentz 1847) or *C. mildei* Koch 1839], all of which were common at the study site.

Incidental observations of *S. vitis* and other spiders in vegetation in the study site were recorded while taking samples, as well as on other visits. Data on river stages were obtained from the California Department of Water Resources (2013) for the American River at H Street (HST) station, 4 miles downstream from the study site. Because sample sizes used in most pairwise comparisons were fairly small, I used Fisher's Exact Test to evaluate statistical significance.

Results

Patterns of occupancy in exuviae. A total of 395 exuviae were either opened and examined in the field or collected and monitored for signs of occupancy by invertebrates. Two libellulid species, *Libellula luctuosa* (N = 142) and *Tramea lacerata* (N = 147), accounted for 73.2% of the exuviae sampled. Exuviae of an aeshnid, *Anax junius*, were 10.7% (N = 42) of the total. Exuviae of *Plathemis lydia* and exuviae not

positively identifiable as either *P. lydia* or some species of *Libellula* (including *L. pulchella* Drury 1773, *L. forensis* Hagen 1861, and *L. luctuosa*) together comprised another 10.7% (N = 42). The remaining 22 exuviae examined were of an assortment of the gomphids *Stylurus olivaceus* (Selys 1873) and *Ophiogomphus occidentis* Hagen 1885, and the libellulids *Erythemis collocata* (Hagen 1861), *Pachydiplax longipennis* (Burmeister 1839), *Pantala hymenaea* (Say 1839), and *Sympetrum corruptum* (Hagen 1861) (Table 1).

Table 1. Occupancy of various odonate exuvia types by spiders and other arthropods at backwater lagoons in the floodplain of the American River, Sacramento County, California.

		<i>Libellula luctuosa</i>	<i>Plathemis lydia</i>	<i>Libellula</i> or <i>Plathemis</i>	<i>Tramea lacerata</i>	<i>Anax junius</i>	<i>Pantala hymenaea</i>	<i>Ophiogomphus occidentis</i>	<i>Stylurus olivaceus</i>	<i>Erythemis collocata</i>	<i>Pachydiplax longipennis</i>	<i>Sympetrum corruptum</i>	unidentified libellulid	TOTAL
<i>Sassacus vitis</i>	♂♀ in retreat	1	1		1									3
	♀ in retreat	3	1	2		1								7
	♂ in retreat	2	1											3
	immature in retreat	1												1
	nest or ♀ in nest	23	1		8	1	1							34
	exuvia in molt sac	2				1								3
	TOTAL <i>S. vitis</i>	32	4	2	9	3	1	–	–	–	–	–	–	51
other salticid spiders	<i>Peckhama</i> sp. ♀ in nest	1												1
	<i>Sitticus palustris</i> ♀ in nest	1												1
	<i>Synageles occidentalis</i> ♀ in nest	1		1	1									3
other spiders	unidentified spider nest	1			1									2
	subadult araneid				1	1								2
	immature thomisid		1		1									2
	subadult <i>Cheiracanthium</i> sp.	2			3									5
	small unidentified spider				1									1
other arthropods	alleculine beetle					1								1
	elaterid beetle	1												1
	phalacridid beetle	2		1										3
	two small beetles			1										1
	<i>Boisea</i> cf. <i>rubrolineata</i> nymph		1											1
	unidentified insect nymph					1								1
	unidentified insect remains in cocoon				1									1
traces of non-arachnid cocoon	1												1	
TOTAL other than <i>S. vitis</i>	10	2	3	9	3	–	–	–	–	–	–	–	–	27
empty retreat	15	3	5	8	2	–	–	–	–	–	–	–	–	33
unoccupied	85	9	14	121	34	–	1	11	2	5	1	1	1	284
TOTAL	142	18	24	147	42	1	1	11	2	5	1	1	1	395

Of these 395 exuviae, 28.1% (N = 111) were occupied or showed signs (*e.g.*, unoccupied retreats, cocoon remnants) of being used by arthropods. Only 13 (3.3%) of all exuviae contained non-arachnid arthropods other than egg parasitoids, and three of these also contained *Sassacus vitis* or evidence of occupancy by a salticid (empty retreat). These arthropods were a mix of insects, including 8 beetles, 2 unidentified pupal remains, 1 hemipteran nymph (probably *Boisea rubrolineata* [Barber 1956]), and 1 unidentified insect nymph (which hopped out of an exuvia when picked up and was lost). Insects (other than egg parasitoids) were found in exuviae in only two of the five survey years, and only in samples collected in May or the first half of June.

Most (91%, N = 101 of 111) of the occupied exuviae contained spiders or spider retreats. About 50% (51 of these 101) were occupied by *Sassacus vitis*. Thirty-four of the exuviae inhabited by *S. vitis* contained nests (retreats with egg sacs), almost invariably with an attending female (31 of 34, or 91%), but some contained single adult males or females, occasional pairs, spider molt exuviae (i.e., molt retreats), or individual sub-adults. Another 33 (33%) of the 101 exuviae showing signs of spider occupancy contained unoccupied spider retreats. I collected exuviae during the late morning and early afternoon, when salticids often leave their roosts to hunt. Unoccupied retreats collected during midday are probably more likely to belong to diurnal hunters (e.g., salticids) than to nocturnal hunters (e.g., *Cheiracanthium* spp.). As *S. vitis* was by far the most frequently-encountered spider in exuviae, a large proportion of the empty retreats I collected probably belonged to that species.

Dates on which *Sassacus vitis* were encountered in exuviae ranged from 2 May to 25 September, encompassing the entire span of dates surveyed. On only 4 survey dates – 10 June 2008, 22 June 2009, 18 August 2009, and 13 July 2010 – were no *S. vitis* found in exuviae, but an unoccupied retreat, possibly belonging to that species, was found on one of these dates, and an unguarded salticid egg sac, also possibly belonging to *S. vitis*, was found on another.

Seventeen of the 101 exuviae with evidence of spider occupancy contained a mix of spider species other than *Sassacus vitis*. Three other salticid species, all females with egg sacs, were found in 5 exuviae: three *Synageles occidentalis* Cutler 1988, an undescribed *Peckhamia* sp., and a *Sitticus palustris* (Peckham & Peckham 1883). One other exuvia contained an egg sac, almost certainly of a salticid, but it had no attendant female and only produced egg parasitoids (*Idris* sp.), so the species of spider could not be determined. Only 11 exuviae contained non-salticid spiders: 5 *Cheiracanthium* sp., 2 thomisids, 2 araneids, and 2 spider sp. (most of these were very small sub-adults, thus difficult to identify). In most instances, except for the *Cheiracanthium*, non-salticid occupants seemed to have been mere transients (i.e., no retreats were present). The *Cheiracanthium* were all sub-adults (thus not identifiable to species) of various sizes, which produced retreats and occasionally molted in odonate exuviae. In one instance the remains of a non-salticid spider egg sac was found.

Occupancy by *Sassacus vitis* varied among different exuvia types. These differences were fairly consistent from year to year (Figure 5), despite the fact that there were significant differences in water level variation, and hence in the timing of my survey effort, in different years (Figure 4). For the two species with the largest sample sizes, *Libellula luctuosa* and *Tramea lacerata*, I found no significant difference in occupancy by *S. vitis* within species between any two years (Fisher's Exact Test, $P \geq .05$), but there were significant differences between species within three years (2008, 2009, 2010), which were the three years with, probably not coincidentally, the largest sample sizes (Fisher's Exact Test, $P \leq .05$; Figure 5). Combining data for all years, *L. luctuosa* exuviae were used by *S. vitis* to a significantly greater extent than were *T. lacerata* exuviae (Fisher's Exact Test, $P \leq .05$; Figures 5 and 6). Levels of occupancy in *T. lacerata* and *Anax junius* exuviae were not significantly different (Fisher's Exact Test, $P \geq .05$; Figures 5 and 6). I also calculated percent of *S. vitis* occupancy in all unidentified *Libellula* sp. and *Plathemis lydia* exuviae combined, as all these exuviae are very similar in size and appearance, differing only in minor aspects of external morphology (e.g., the fine crenulation of labial segments). Percent occupancy by *S. vitis* in all *Libellula/Plathemis* exuviae (excluding exuviae positively identified as *L. luctuosa*) did not differ significantly from that in *L. luctuosa* exuviae (Fisher's Exact Test, $P \geq .05$; Figure 6).

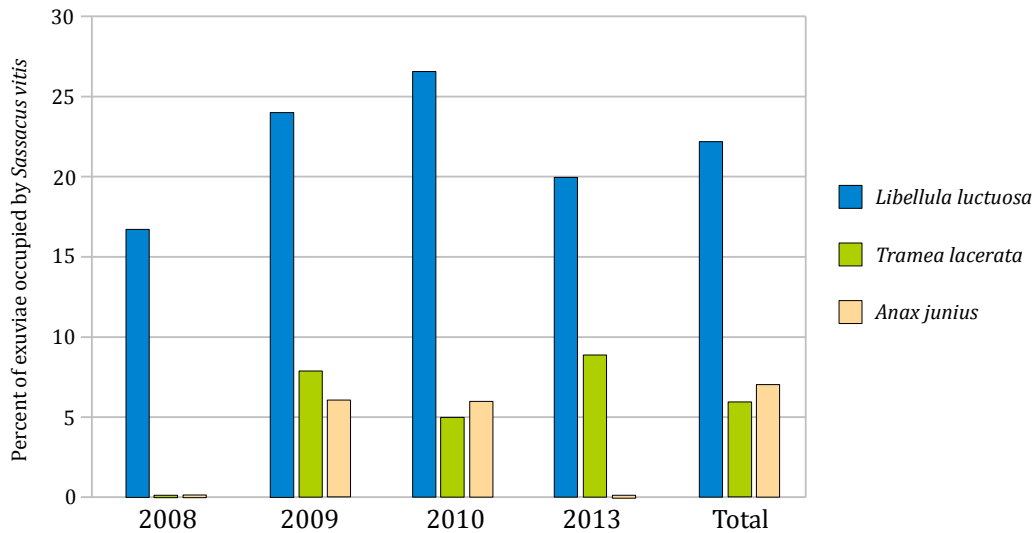


Figure 5. Percent occupancy by *Sassacus vitis* in the exuviae of three species of dragonflies (*Libellula luctuosa*, *Tramea lacerata*, and *Anax junius*) collected along the American River Parkway, Sacramento County, California, in four different years and for the entire duration of this study. Data for 2012 are included in the total.

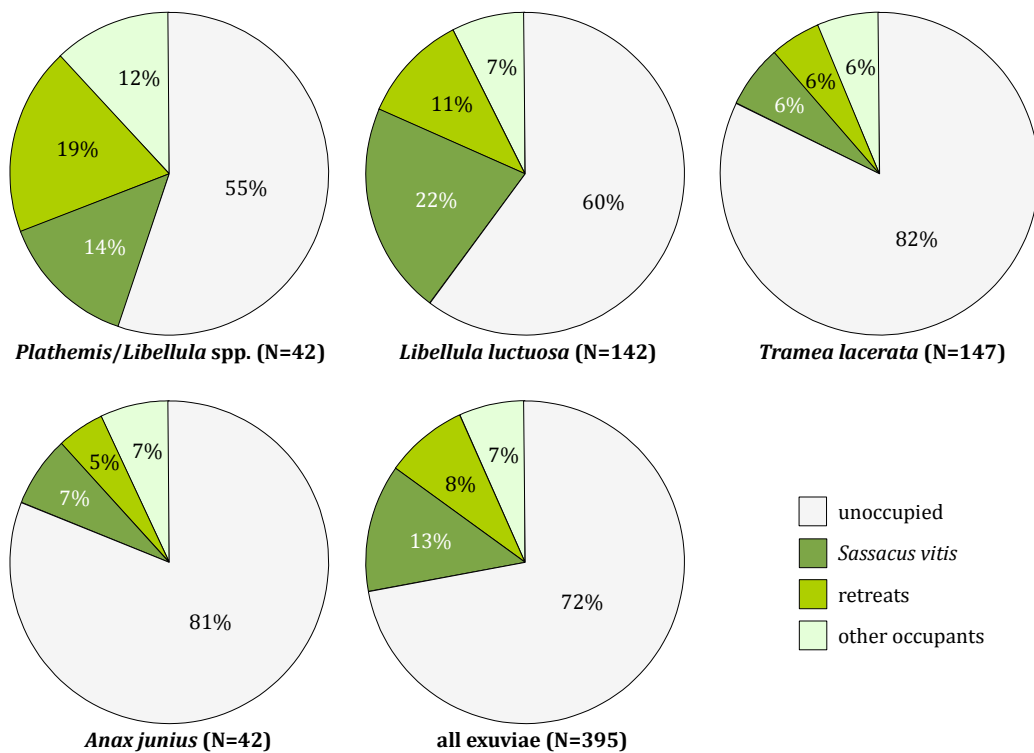


Figure 6. Occupancy patterns for the most commonly-encountered exuvial types, and all exuviae, collected along backwater lagoons of the American River, Sacramento County, California, for all years of the study combined. The data for “*Plathemis/Libellula* spp.” refers to the data for *P. lydia* and undetermined *Plathemis/Libellula* exuviae combined, excluding *L. luctuosa* data.

The average dimensions of the abdominal cavities of exuviae of *L. luctuosa* and *T. lacerata* are fairly close fits for the average dimensions of *S. vitis* nest retreats found, primarily in crevices in bark, by Vetter and Carroll (2013) (Table 2, Figure 7). Dimensions of *P. lydia* exuviae are a bit tighter, those of *A. junius* are more expansive. None of these exuviae would appear large enough to accommodate the nest retreats of *Cheiracanthium* or *Phidippus*, however.

Table 2. Dimensions of abdominal cavities for four species of dragonfly exuviae used by *Sassacus vitis* as nest and roost sites along backwater lagoons of the American River, Sacramento County, California, and dimensions of nest retreats of various spiders from Vetter & Carroll (2013) (*).

SPECIES	N	DIMENSIONS in mm \pm 1 SD	
		LENGTH	WIDTH
<i>Plathemis lydia</i> (exuvial abdomen)	3	11.53 \pm 0.6	6.17 \pm 0.6
<i>Libellula luctuosa</i> (exuvial abdomen)	15	12.22 \pm 0.6	6.76 \pm 0.3
<i>Tramea lacerata</i> (exuvial abdomen)	15	12.23 \pm 1.1	8.88 \pm 0.4
<i>Anax junius</i> (exuvial abdomen)	6	25.27 \pm 1.5	7.72 \pm 0.4
<i>Sassacus vitis</i> (nest retreat)*	10	13.5 \pm 3.4	7.0 \pm 1.8
<i>Cheiracanthium mildei</i> (nest retreat)*	2	25.0 \pm 7.1	17.5 \pm 3.5
<i>Phidippus audax</i> (nest retreat)*	1	33.0	33.0

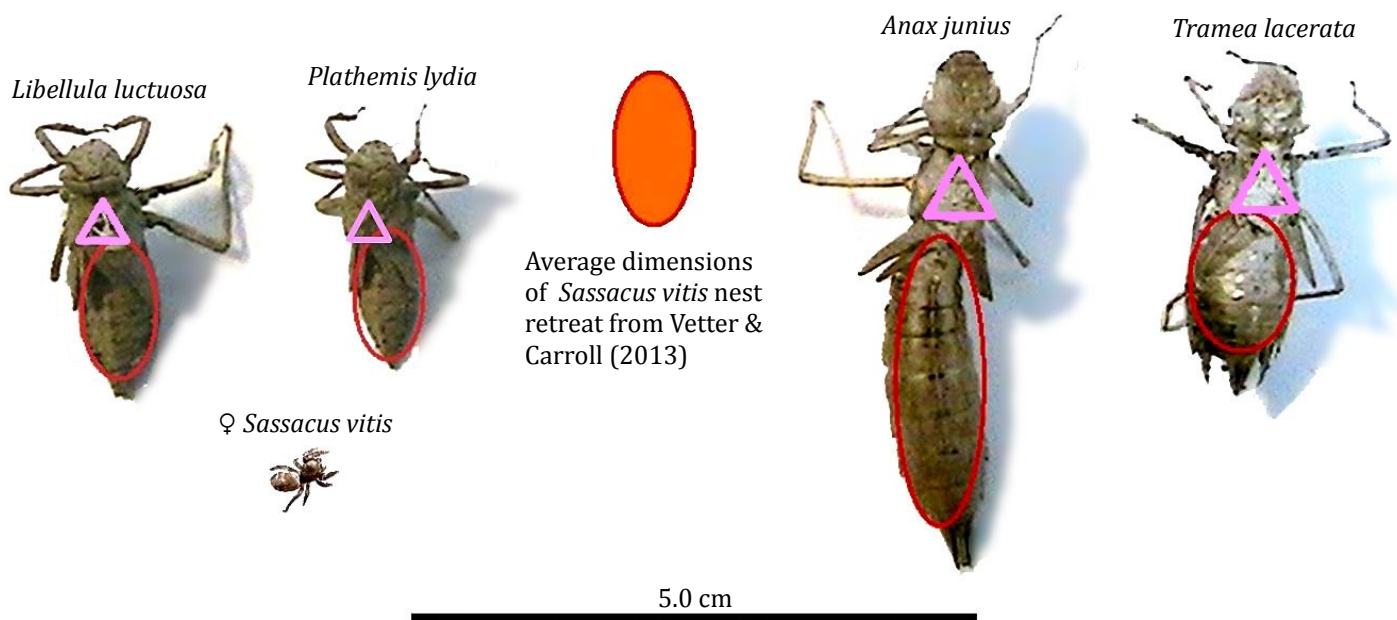


Figure 7. Dragonfly exuvia types commonly encountered along backwater lagoons of the American River, Sacramento, California. Average dimensions of abdominal cavities shown as red ovals, entrance gaps atop thoraces shown as pink triangles.

A small sample (N=16) of spider retreats (none of them nests) were encountered in inflorescences of rushes (15 *Juncus*, 1 *Schoenoplectus*) on three dates in September 2010. Of these, eleven (69%) were occupied by *Phidippus audax*, three (19%) were occupied by *Cheiracanthium*, one was occupied by a *Sassacus vitis*, and two were unoccupied (probably created by salticids based on their structure). Two other retreats were found outside of exuviae: a retreat of a *Cheiracanthium* subadult wedged between an exuvia and a rush inflorescence; and a nest retreat with eggs, presumably of *S. vitis*, on a curled *Iris pseudacorus* leaf within 1 cm of an exuvia occupied by a female *S. vitis* and also containing eggs. Both of the latter *S. vitis* egg clusters produced only brood parasitic wasps (*Idris* sp.).

Breeding biology of Sassacus vitis in exuviae. Although 34 odonate exuviae collected in this study provided evidence of nesting by *S. vitis* (Figure 8) not all of these provided equivalent data. For example, one exuvia of *Plathemis lydia* collected on 2 May 2008 and occupied by a female *S. vitis* was immersed in alcohol before the presence of an egg sac was detected. This nest provided data on clutch size (*i.e.*, the number of eggs in an egg sac) but could not supply information on time to emergence or incidence of parasitism. Hence, sample sizes of nest retreats used in this paper for analyses of various aspects of the breeding biology of *S. vitis* vary slightly. Some special cases will be discussed separately in more detail.



Figure 8. Opened dragonfly exuvia containing the nest retreat of a *Sassacus vitis*, collected along the shoreline of a backwater lagoon in the American River Parkway, Sacramento County, California on 24 May 2008. Note the silk-lined interior of the abdominal cavity. The spider's egg sac is the white mass in the center of the image. Photograph © Ray Bruun.

Except in a few cases, such as the one cited above, it was impossible to measure clutch sizes by counting eggs in egg sacs without damaging the exuvia and their contents. However, I was able to determine clutch size by tallying all emerging spiderlings (and wasps in parasitized nests) and, after all live occupants were deemed to have emerged, by opening exuviae and counting any dead occupants or unhatched eggs. 32 egg sacs in exuviae (including a couple of second clutches laid in captivity) provided such data. For 22 egg sacs that were unparasitized, the average clutch size for *Sassacus vitis* was 15.86 (SD = 5.48, Range 5-29). For 8 egg sacs parasitized solely by *Idris* wasps, counting each wasp emerging from a sac as equal to one spider egg (see below under *Nest parasitism*), average clutch size was 15.88 (SD = 6.79, Range 7-31). The average clutch size for all 32 egg sacs, including two for which presence or absence of wasps could not be determined, was 15.56 (SD = 5.84, Range 5-31). Unhatched eggs were rare. One clutch of 8 eggs failed to develop; possibly these were infertile. In each of two other exuviae, a parasitic wasp failed to emerge successfully from an egg. Year-to-year variation in sample sizes of *S. vitis* egg clutches were too small (*e.g.*, two egg sacs in 2008, four in 2012) for meaningful statistical analysis. For the year with the largest sample size (14 egg sacs in 2010), the average clutch size was 15.6. Annual average clutch size ranged from 13 (2008, N=2) to 19.8 (2013, N=6).

I was able to tally the elapsed time (in days) from date of collection to date of first spiderling emergence for 26 *S. vitis* nests. All spiderlings did not invariably emerge from nests on the same day, but most if not all had emerged within 1-2 days of the first emergence. This time period (observed emergence time, hereafter referred to as OET) ranged from 0 (spiderlings emerged when exuviae first picked up) to 30 days, with considerable variation and no clear peaks (Mean = 13.92 days, SD = 7.82). This suggests that my collecting protocol – collecting all exuviae when first encountered over a period of months, May through September, in a 5-year period – was an indiscriminate sample of nests in regards to stage of embryonic development. The actual time from egg laying to spiderling emergence (actual emergence time, hereafter AET) in *S. vitis* should be close to the high end of my measured OETs.

Observations of a few specific exuvial nests allow a somewhat better estimate of the range of AET. In the first case, an apparently gravid female emerged on the day of collection, and then reappeared 5 days later, much thinner. She thus likely laid eggs in the period between days 1-6. The first emerging spiderlings from this nest appeared on day 25, giving a range of from 19-24 days for AET. Two other collected exuviae containing nests from which spiderlings emerged were unattended by female *S. vitis*, thus the egg clusters in these nests had to have been laid at least one day prior to collection. OETs for these nests were 24 and 26 days. The only nest for which OET was longer than 26 days was a nest with an OET of 30 days. However, the female associated with this nest did not first emerge from the exuvia until day 8. She therefore may have laid her eggs anytime between day 1 and 8. AET for *S. vitis* thus appears to range from at least 19 to at most 30 days, with typical AET probably somewhere around 24-26 days.

Unfortunately, I was not able to observe when eggs hatched in exuviae, as this would have required breaking up the exuviae and the thick coating of silk encasing the egg cluster. In salticids, hatching produces a relatively immobile "post-embryo" stage, followed a number of days later by the molt to the first mobile instar, *i.e.*, dispersing spiderlings (Jackson 1978; Richman & Whitcomb 1981). AET thus equals the incubation period plus the post-embryo stage. There is one published value for the incubation period of *S. vitis*, 17-18 days (Richman 2008). Given an estimate of typical AET at 24-26 days, this provides a range estimate of the post-embryonic stage for this species of from 6-9 days.

Nest parasitism. Of 36 egg sacs found in odonate exuviae in the field for which evidence of parasitism could be determined, 10 (28%) were parasitized (Table 3). All parasitized nest retreats were occupied by *Sassacus vitis* except one, which might have been an *S. vitis* nest retreat. Based on its structure, this latter nest retreat appeared to be that of a salticid, but it was not guarded by a female nor did it produce any spiderlings. The most abundant wasp parasitoid was a distinctive, undescribed species of *Idris* whose females have amber heads and dark, blackish thoraces and abdomens. All but one of the parasitized *S. vitis* clutches were parasitized by this species. The nest retreat of an unidentified salticid was parasitized by an all-dark species of *Idris*. A most remarkable nest retreat, although attended by a female *S. vitis*, was not only parasitized by what appeared to be a third dark species of *Idris* but also produced a male *Gelis* sp. The latter wasp may well have engaged in hyperparasitism, eating *Idris* larvae as well as spider embryos within the eggs it devoured, but five adult *Idris* (a male and four females) and a single spiderling managed to emerge from this nest retreat as well. Another spiderling was found dead in the egg sac when the exuvia was opened. In this instance, of course, the original spider clutch size and percent of eggs parasitized by *Idris* could not be determined.

In the eight exuvial nest retreats of *Sassacus vitis* parasitized by the amber-headed *Idris* sp. in the field, the percent of all eggs parasitized ranged from 16.7 to 100. Two of these egg sacs produced only wasps, three produced more wasps than spiders, and three produced more spiders than wasps. The average numbers of wasps and spiders produced per parasitized egg sac were 10.375 and 5.5, respectively. There appeared to be no striking impact of nest attendance by female *S. vitis* on incidence of parasitism by *Idris* sp. Seven of twenty-six (27%) attended nest retreats were parasitized, compared to one of three (33%) unattended ones, but sample sizes are too small for meaningful statistical analysis. The presence of *Idris* did not seem to affect the OET of spiderlings. OET averaged 13.4 days for 5 parasitized egg sacs (range 4-21) and 14.05 days for 21 unparasitized egg sacs (range 0-30). Sample sizes were also too small for analysis of possible effect of exuvia type on frequency of parasitism, but the data for *Libellula luctuosa* and *Tramea lacerata* (Table 3) suggest that exuviae of the latter species might be more susceptible to parasitism. Additional aspects of the breeding biology of the amber-headed *Idris* sp. will be discussed in another paper.

Table 3. Impact of wasp parasitism on salticid nests in exuviae collected along backwater lagoons of the American River, Sacramento County, California. "Other" exuviae include one each of *Plathemis lydia*, *Pantala hymenaea*, *Anax junius*, and *Libellula* sp.

	<i>Libellula luctuosa</i>	<i>Tramea lacerata</i>	other
unparasitized	18	4	4
parasitized	6	4	—
% parasitized	25%	50%	—
spiderlings per parasitized nest	5.83	2.5	—

Other salticids in exuviae. Three other salticid species were found nesting in odonate exuviae in this study, and as even basic life history data for many salticids is scarce or lacking in the published literature, I report these here.

A female *Sitticus palustris* emerged from an exuvia of *Libellula luctuosa* collected on 22 June 2009. She was very fat, apparently gravid, but was not seen subsequently out of the exuvia until the first spiderlings were seen on 17 July. Unfortunately, I had been out of town from 8 July until 17 July, and as some of the spiderlings found outside of the exuvia on the latter date were already dead, first emergence had probably been some days earlier. Fourteen spiderlings eventually emerged from this clutch.

A female *Peckhamia* sp., an undescribed western North American sister species of *P. americana* (Peckham & Peckham 1892) fide B. Cutler, was collected in an exuvia of *L. luctuosa* on 20 July 2010. This exuvia was in a somewhat atypical location, on a mugwort (*Artemisia douglasiana*) about 20 cm above ground and 0.5 m from the shoreline. This was the only exuvia I found on mugwort, a plant on which I have frequently observed *Peckhamia* sp. at this site. The female ate a small leafhopper given it on 21 July, and a small fly provided on 29 July. She was found dead in the vial on 13 August. Two spiderlings emerged from the exuvia when I manipulated it that day. Three more spiderlings had emerged by 17 August, and all had died by 22 August.

On 22 May 2013, each of three exuviae found along a 5 m stretch of shoreline vegetation bordering the large backwater pond at the site was found to contain a female *Synageles occidentalis*. Each female was provided with a small fly every few days. One female, occupying an exuvia of *Tramea lacerata*, died on 19 June. Three spiderlings emerged in the period 24-26 June; all had died by 3 July. Another female, in an exuvia of *L. luctosa*, was still alive when two spiderlings emerged 26-27 June. The female died on 2 July. One infertile egg was found in this exuvia. The third female, in an exuvia of a *Libellula* sp., died on 10 June. Three spiderlings emerged on 24 June. A total of nine had emerged by 29 June, all of which were dead by 3 July.

Discussion

Properties of an exuvia that might influence its selection by a spider fall into two major categories: structural and situational. Structural properties include size, shape, pigmentation and the degree to which an exuvia is coated with debris and sediments. Structural properties are for the most part determined by the life histories and habitats of larvae of different species. Situational properties include the substrate on which the exuvia is found (on the ground, on a log, on a particular species of plant, etc.) height above the ground or water, and distance from the shoreline. These two categories are sometimes, but not always, correlated, as different species of dragonflies often select different sites for their emergence. For example, gomphids (*Stylurus olivaceus*, *Ophiogomphus occidentis*, *Gomphus kurilis* Hagen in Selys 1858) that breed in the American River differ from the other dragonflies observed in this study in

that they emerge, for the most part, on the barren shore line of the main river channel. In addition to the small sample of gomphid exuviae found during my surveys (Table 1) I sampled an additional 12 exuviae of *O. occidentis* and *G. kurilis* along the shoreline of the river opposite from my study site on 14 May 2008. None of the gomphid exuviae I examined contained spiders or any other arthropods. Being exposed on bare or sparsely-vegetated ground, where they are more susceptible to even small changes in water levels than are exuviae higher up in vegetation, may render these exuviae less desirable as potential domiciles for arthropods.

Using the categories defined by Corbet (1999), three types of dragonfly larvae can be identified among the species encountered in this study. *Anax junius* is an active clasper, crawling on submerged vegetation in search of prey. *Tramea lacerata* and *Pantala hymenaea* are active sprawlers, which walk and run on long legs in search of prey. These two types of active hunters, though differing in body shape and relative leg length, share similarities in color pattern (mottled but not heavily pigmented) and external texture (smooth and non-setose). Their exuviae are typically clean and nearly transparent (Figure 6). *Plathemis lydia* and *Libellula* species encountered in this study are shallow burrowers, which lie partially buried in bottom sediment waiting for prey to pass by. They have structurally similar, moderately to heavily-pigmented bodies. They are strongly setose on the dorsal surfaces. These setae retain particles of sediments and other debris, even algal growths, which form a dense, opaque encrustation on dry exuviae (Figure 6).

The size and shape of a dragonfly exuvia will limit the types of occupants it can accommodate as well as the uses to which it may be used by occupants. For a spider, the first hurdle is the size of the entry hole, the slit atop the thorax from which the dragonfly emerged (Figure 6). Additional constraints are the dimensions of the exuvial abdominal cavity. In this study, *Sassacus vitis* demonstrated the capacity to use exuviae as small as those of *P. lydia* for retreats, including nest retreats. Probably any small salticids (in the range of 3-5 mm adult body length) that inhabit low, herbaceous vegetation near bodies of water (*e.g.*, *Sibianor aurocinctus* [Ohlert 1865] [Torralba-Burrial et al. 2007]) are similarly able to utilize exuviae for these purposes. The smaller subadults of larger spiders such as *Cheiracanthium* spp. and *Phidippus* spp. may be able to use exuviae for retreats, but adult body sizes and clutch sizes of these species (see Vetter & Carroll 2013) render use of exuviae for nesting difficult, if not impossible.

Situational properties were more difficult to evaluate than were structural properties, and I did not collect situational data at the beginning of my study. Because I collected exuviae as they were found, the only data (*e.g.*, height above ground /water and distance from the shoreline) I could record were for the date of collection. But, as water levels often changed over relatively short periods of time – one or two weeks – during the course of a field season, such data were impossible to determine for the dates of dragonfly emergence or for the dates of initial occupancy by spiders. Situational properties certainly deserve more thorough investigation, however.

While a seemingly random assemblage of insects and spiders (other than *Sassacus vitis*) were encountered as occasional occupants of dragonfly exuviae at a single site over a 5-year period, one clear pattern did emerge: persistent and frequent use of exuviae by *S. vitis*. A number of aspects of this species' use of exuviae suggest that it is deliberate and selective. First, the frequency of occupancy was fairly consistent from year to year, despite differences in the timing of changes in water levels and the emergence of dragonflies. Second, *S. vitis* were observed in exuviae in essentially all stages of their life cycle (as sub-adults, as single adult males or females, in pairs, during molt, and while nest guarding). Third, *S. vitis* demonstrated a significant preference for using the exuviae of burrowers (*L. luctuosa* and *P. lydia*) versus those of claspers or sprawlers (*T. lacerata* and *A. junius*). While possible differences in situational properties of these various types of exuviae cannot be ruled out as influencing their

desirability to *S. vitis*, there are a number of reasons for considering structural properties as important determinants. In particular, increased opacity and encrustation could provide insulation from thermal extremes and evaporative water loss by egg sacs on hot summer days, in addition to providing increased structural integrity (Figure 8). Tyrrell (2004) commented that he found dark and opaque exuviae were occupied by spiders and other arthropods whereas paler and more transparent exuviae, even of the same species of dragonfly, were not occupied. The salticid *Sibianor aurocinctus* (Ohlert 1865), found inhabiting and breeding in exuviae in Spain by Torralba-Burrial *et al.* (2007), occupied exuviae of *Orthetrum brunneum* (Fonscolombe 1837), whose larvae are shallow burrowers similar in appearance to *Libellula* species.

Use of exuviae by *Sassacus vitis* may be fairly widespread, at least in the Pacific States. A request made to odonatologists for observations of spiders using exuviae (Manolis 2008) produced a modest response, but most such observations involving salticids were of *S. vitis* and they came from a broad geographic area, including three scattered locations in Oregon and two additional locations in California, one near the Oregon border in Siskiyou County and one near the Mexican border in San Diego County (Figure 9; details in Manolis 2013). The California reports were of *S. vitis* using exuviae of *Plathemis lydia*.

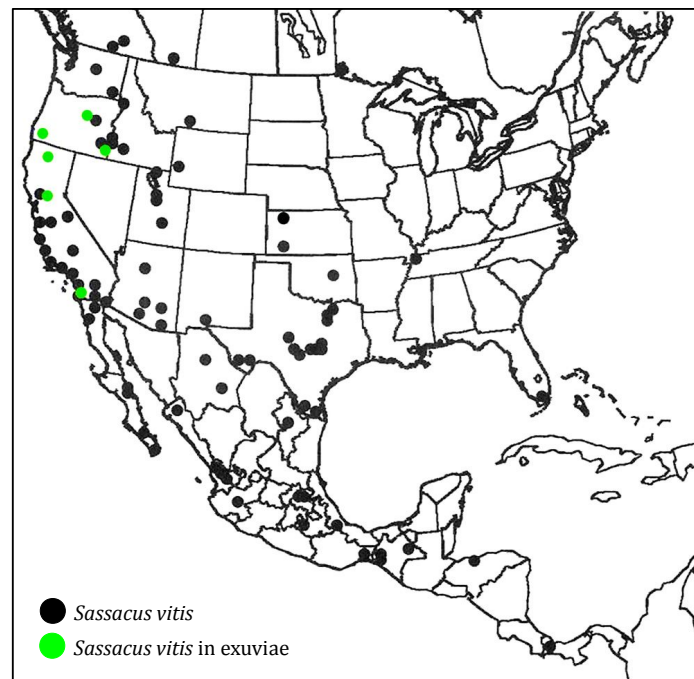


Figure 9. Distribution of *Sassacus vitis* (black circles) and locations where *S. vitis* has been collected in odonate exuviae (green circles; see text for details). Map adapted from Richman (2008).

Sassacus vitis is a common and widespread species in western North America (Richman 2008; Figure 9). It occupies a wide range of habitats, including alfalfa fields, grasslands, rice fields, marshes, vineyards, orchards, suburban gardens, open woodlands, and riparian brush and brambles (Oraze *et al.* 1988; Richman 2008; Carroll 2012, pers. obs.). The little that is known of its life history and breeding biology prior to this study comes primarily from research on its status in crops, especially grapes, in the San Joaquin Valley of California (Costello & Daane 1995; Costello *et al.* 1996; Vetter & Carroll 2013). Retreats and nests of this species in these agricultural situations are found primarily in crevices of bark, although grape bunches and floral inflorescences are also used (Carroll 2012). As noted earlier, the size and shape (ellipsoid) of retreats, including nests with eggs, of this species and other small salticids found in these

situations is very similar to the size and shape of the abdominal chambers of many dragonfly exuviae. Often salticid retreats have lip-like openings at either end of the major axis of the ellipsoid, but in situations such as odonate exuviae, there is only an opening at one end of this axis, at the base of the tear atop the exuvial thorax from which the dragonfly emerged (Figure 7). This entrance is guarded by the female spider.

Average clutch sizes of *Sassacus vitis*, obtained from nest retreats in agricultural situations (Vetter & Carroll 2013) and from a small sample of clutches laid in captivity (Richman 2008) are smaller than the average obtained in this study (Table 4), despite the fact that the dimensions of exuvial nests are implacably limited by the abdominal cavity walls (Table 2, Figure 7). Such comparisons between studies of different populations must be viewed with caution. *S. vitis* females produce more than one clutch and, though data are limited, appear to produce subsequent clutches of decreasing size (pers. obs.). Thus, for comparisons between studies to be meaningful, clutches of equivalent laying order should be compared. The two largest clutch sizes obtained in this study (29 and 31), however, are about 1.5 times the maximum obtained by Vetter & Carroll (2013), who wrote that “an egg sac containing 30 eggs would surely exclude . . . *Sassacus vitis*.”

Table 4. Average clutch sizes in egg sacs of *Sassacus vitis* from three sources: (1) odonate exuviae (this study), (2) agricultural environments in the San Joaquin Valley (Vetter & Carroll 2013), and (3) a small sample of clutches laid in captivity (Richman 2008).

CLUTCH SIZE	SOURCE		
	this study	Vetter & Carroll (2013)	Richman (2008)
average	15.56	12	12.4
SD	5.84	3.37	1.95
minimum	5	5	10
maximum	31	18	15
N	32	17	5

The presence of exuviae in emergent, shoreline vegetation appears to provide *Sassacus vitis* with the opportunity to establish viable populations in an environment that is probably rich in food resources but depauperate in structural complexity. Halaj *et al.* (2000) showed that providing artificial, modular habitat refugia markedly increased spider densities in soybean fields, and a similar phenomenon may be at work in this case. Interspecific competition for roost and nest sites is reduced because the dimensions of most exuviae exclude their use by other common, larger spiders in these habitats (*e.g.*, *Phidippus audax*, adult *Cheiracanthium*). Selective use of certain types of exuviae (*e.g.*, smaller, darker and encrusted ones) may provide protection from predation on adults, eggs and spiderlings by these larger spiders or other predators, including nest parasitoids.

Observations of spiders using exuviae made by Tyrrell (2004), Torralba-Burrial *et al.* (2007), Jäckel & Koch (2015), Kunz (2010), and Wieland (2015) suggest that this behavior may be widespread, practiced by different spiders, not all of them salticids, in different wetland habitats in different parts of the world. For example, Tyrrell (2004) in England and Jäckel & Koch (2015) in Germany found *Clubiona* spp. to be the most common inhabitants of odonate exuviae. These spiders are similar to *Cheiracanthium* spp. in that adults are typically larger than salticids the size of *S. vitis* and produce larger egg sacs. Both studies noted that these *Clubiona* spp. could roost in exuviae of smaller odonate species (*e.g.* *Libellula quadrimaculata* Linnaeus 1758), but showed a strong preference for nesting in exuviae of larger species in the genera *Anax* and *Aeshna*. Further study of the consistent use of odonate exuviae by certain species of spiders is certainly warranted in order to increase understanding of this phenomenon. Data on breeding biology, such as breeding phenology and host/parasite relationships, of most salticids is poorly known or non-

existent, in part because finding nests can prove very difficult and time consuming. However, as this study has shown, identifying species such as *S. vitis* as frequent users of odonate exuviae provides an opportunity to collect such data relatively easily and in sufficient quantities for useful analyses. Finally, the use of exuviae by salticids such as *S. vitis* opens the door for laboratory experiments on factors involved in nest site selection by salticids and the extent to which this may be learned behavior.

Acknowledgements

I am most grateful to Mark Tyrrell, Antonio Torralba-Burrial, Kathrin Jäckel, Kamilla Koch, Johanna Wieland, and Fred SaintOurs for providing information on their research and observations of spider occupancy of odonate exuviae, to Steve Krotzer, Kathy Biggs, Jim Johnson, and Gary Suttle for providing specimens of spiders found in exuviae, to David Richman, Richard Vetter, and Devin Carroll for supplying information on aspects of breeding biology of *S. vitis*, to Ray Bruun for allowing me to use his photographs of *S. vitis* and its nest, to Lubomir Masner and Robert Zuparko for identification and information concerning hymenopteran parasitoids, to Bruce Cutler for information about the undescribed species of *Peckhamia* I encountered, and to Annette Manolis, my wife, for her unflinching support. Finally, David Hill, Kamilla Koch, David Richman, and Ken Schneider provided critical reviews of early drafts of this paper.

References

- Araujo, D. P., and M. De Maria. 2008.** Nesting of jumping spiders (Araneae, Salticidae) inside abandoned wasps nests (Hymenoptera, Aculeata). *Revista Brasileira de Zoociências* 10:171-173.
- Boulton, A. M., and G. A. Polis. 2002.** Brood parasitism among spiders: interactions between salticids and *Diguetia mojavea*. *Ecology* 83: 282-287.
- California Department of Water Resources. 2013.** California Data Exchange Center – Stations. Online at <http://cdec.water.ca.gov/staInfo.html>, accessed on 24 JAN 2014.
- Carroll, D. 2012.** Spiders in San Joaquin Valley vineyards: pests, biters, and IPM agents. Online at <http://aaie.net/wp-content/uploads/2013/01/Spiders-in-San-Joaquin-Valley-Vineyards-2012.pdf> accessed on 18 JAN 2016.
- Corbet, P. S. 1999.** Dragonflies: behavior and ecology of Odonata. Cornell University Press. Ithaca, N. Y.
- Costello, M. J., and K. M. Daane. 1995.** Spider (Araneae) species composition and seasonal abundance in San Joaquin Valley grape vineyards. *Environmental Entomology* 24: 823-831.
- Costello, M. J., M. A. Mayse, K. M. Daane, W. A. O'Keefe, and C. B. Sisk. 1996.** Spiders in San Joaquin Valley grape vineyards. University of California Division of Agriculture and Natural Resources Leaflet #21530.
- Eason, R. R., W. B. Peck, and W. H. Whitcomb. 1967.** Notes on spider parasites, including a reference list. *Journal of the Kansas Entomological Society* 40: 422-434.
- Edwards, G. B. 1990.** Anecdotal field notes on Florida *Phidippus* (Araneae: Salticidae), with notes on territoriality in *P. regius*. *Peckhamia* 2 (6): 96-100, *Peckhamia* 66.1.
- Fitton, M. G., M. R. Shaw, and A. D. Austin. 1987.** The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society, London* 90: 65-93.
- Halaj, J., A. B. Cady, and G. W. Uetz. 2000.** Modular habitat refugia enhance generalist predators and lower plant damage in soybeans. *Environmental Entomology* 29: 383-393.
- Howard, L. O. 1890.** Two spider-egg parasites. *Insect Life* 2: 269-271.
- Hutchinson, R., and B. Ménard. 2013.** Spiders collected in odonata exuviae in the province of Quebec. *Argia* 25: 18.
- Jackson, R. R. 1978.** The life history of *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology* 6: 1-29.
- Jackson, R. R. 1979.** Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, patterns of occupation, and function. *Journal of Arachnology* 7: 47-58.
- Jäckel, K., and K. Koch. 2015.** Anisoptera-Exuvien (Odonata): nur leere Hüllen? *Libellula* 34 (3/4): 143-159.
- Jennings, D. T., B. Cutler, and B. Connery. 2008.** Spiders (Arachnida: Araneae) associated with seed heads of *Sarracenia purpurea* (Sarraceniaceae) at Acadia National Park, Maine. *Northeastern Naturalist* 15: 523-540.
- Johnson, S. R. 1995.** Nests of *Hibana gracilis* are reused by *Phidippus clarus* in wetlands of northeastern Kansas. *Journal of Arachnology* 23: 44-45.

- Judd, W. W. 1967.** Insects and other arthropods from year-old galls caused by *Gnorimoschema gallaesolidaginis* Riley (Lepidoptera: Gelechiidae) on goldenrod. Canadian Journal of Zoology 45: 49-56.
- Kunz, B. 2010.** Ein ungewöhnliches Zuhause: Brutfürsorge der Krabbenspinne (*Xysticus cristatus*) in einer Vierfleck-Exuvie (*Libellula quadrimaculata*). Mercuriale – Libellen in Baden-Württemberg 10: 51-52.
- Manolis, T. 2008.** Spiders residing in odonate exuviae – an update and request for information. Argia 20:19.
- Manolis, T. 2013.** Spiders residing in odonate exuviae: another update and request for more information. Argia 25:24.
- Mikulska, I. 1961.** Parental care in a rare spider *Pellenes nigrociliatus* (L. Koch) var. *bilunulata* (Simon). Nature 190:365-366.
- Miller, W. E. 1966.** Spiders in old insect galls on goldenrod. Ohio Journal of Science 66: 618-619.
- Oraze, M. J., A. A. Grigarick, J. H. Lynch, and K. A. Smith. 1988.** Spider fauna of flooded rice fields in northern California. Journal of Arachnology 16:331-337.
- Richman, D. B. 2008.** Revision of the jumping spider genus *Sassacus* (Araneae, Salticidae, Dendryphantinae) in North America. Journal of Arachnology 36: 26-48.
- Richman, D. B., and R. R. Jackson. 1992.** A review of the ethology of jumping spiders (Araneae, Salticidae). Bulletin of the British Arachnological Society 9: 33-37.
- Richman, D. B., and W. H. Whitcomb. 1981.** The ontogeny of *Lyssomanes viridis* (Walckenaer) (Araneae: Salticidae) on *Magnolia grandiflora* L. Psyche 88: 127-133.
- Torralla-Burrial, A., V. X. Melero, and F. J. Ocharan. 2007.** Utilización de exuvias de *Orthetrum brunneum* (Fonscolombe, 1837) (Odonata: Libellulidae) como lugar de cría por *Sibianor aurocinctus* (Ohlert, 1865) (Araneae: Salticidae). Boletín Sociedad Entomológica Aragonesa 41: 344.
- Tyrrell, M. 2004.** Dragonfly exuviae as accommodation for other insect groups. Dragonfly News 46: 27.
- Vetter, R. S., and D. P. Carroll. 2013.** An identification key for eggs and egg sacs of spiders of potential agro-economic importance: a feasibility study. Journal of Arachnology 41: 176-183.
- Wieland, J. 2015.** Libellenexuvien als Mikrohabitat. Diplomarbeit, Universität Mainz.