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Aquatic insects as umbrella species for ecosystem protection in Death Valley National Park

Noah K. Whiteman · Robert W. Sites

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Abstract Under the United States Endangered Species Act (ESA), critical habitat for listed species is also protected. Many aquatic insects protected under the ESA are habitat-restricted, mainly to springs. Some of these species do not co-occur with ostensibly more charismatic vertebrates, and have the potential to act as umbrella species for aquatic ecosystems. We suggest that the flightless creeping water bug *Ambrysus funebris* La Rivers (Insecta: Heteroptera: Naucoridae) has the potential to be such a species. Endemic to a spring system in Death Valley National Park, it co-occurs with eight other endemic aquatic invertebrate species, but with no vertebrates. Therefore, its protection would facilitate protection of this desert oasis. *Ambrysus funebris* is a candidate for protection under the ESA because of its endemicity, a decline in abundance, and habitat degradation. To facilitate its use as an umbrella species, we report the first illustrated descriptions of the five nymphal instars of *Ambrysus funebris* La Rivers. Recommendations on its conservation and role as an umbrella species for conserving its habitat are presented. A synopsis of aquatic insect species protected or listed as candidates under the ESA indicates that spring-endemics predominate. We also present a list of potentially threatened and unprotected aquatic heteropterans in the western United States.

Keywords Flagship · Invertebrate conservation · Endangered Species Act · Naucoridae · Springs

N. K. Whiteman (✉)
Department of Biology, University of Missouri-St. Louis, 223 Research Building, 8001 Natural Bridge Road, St. Louis, MO 63121, USA
e-mail: nwhiteman@oeb.harvard.edu

R. W. Sites
Enns Entomology Museum, Division of Plant Sciences, University of Missouri-Columbia, 1-31 Agriculture Building, Columbia, MO 65211, USA

Present Address:
N. K. Whiteman
Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

Introduction

In principle, flagship or umbrella species serve as surrogates for protection of other taxa sharing the same habitat (Frankel and Soulé 1981; Landres et al. 1988). Many umbrella species happen to be apex vertebrate predators and debate continues over whether or not these species can actually be used to effectively conserve the ecosystems or habitats in which they reside (Ozaki et al. 2006; Sergio et al. 2006). In situations where ostensibly more charismatic vertebrates are absent as residents, invertebrates have also been employed as umbrella species, and the butterflies (Lepidoptera, Rhopalocera) have served most frequently in that role in terrestrial systems (Launer and Murphy 1994; New 1997).

Members of the Naucoridae (creeping water bugs) are predaceous insects common to aquatic systems in the southwestern United States and tropics. In the United States, the genus *Ambrysus* contains 17 species (Sites and Bowles 1995) and is the most species-rich of the naucorid genera found there. All known species of *Ambrysus* in the United States occur west of the Mississippi River (La Rivers 1950a, 1951), three of which are endemic and restricted to outflows from three thermal spring complexes along or proximal to the Amargosa River drainage on the Nevada-California border. These thermal endemics are brachypterous, flightless, and are the smallest members of the genus (Polhemus 1979; Polhemus and Polhemus 1994). The springs presently occupied by these naucorids may have been interconnected during the Pleistocene epoch (10,000–20,000 years ago) (Soltz and Naiman 1978; Miller 1981) and some springs within the Death Valley region may have been connected as recently as several 100 years before present (Soltz and Naiman 1978). The phylogenetic relationships among these three species are unknown. Three endemic pupfish species in the genus *Cyprinodon* also occupy isolated spring systems near Death Valley; their evolutionary origin, relationships among the three species and populations within species have been the focus of intense study (Duvernell and Turner 1998; Martin and Wilcox 2004; Echelle et al. 2005), while the invertebrate fauna from these and other nearby springs has received less attention from evolutionary biologists (Myers et al. 2001; Sada 2001).

Species associated with springs predominate in the list of currently protected aquatic insect species and candidates for protection under the United States Endangered Species Act (ESA) (Table 1). Many of these species are found exclusively in the arid southwestern United States, an area of high endemism for aquatic insects (Polhemus and Polhemus 2002). Of particular note, *Ambrysus amargosus* La Rivers is restricted to Point of Rocks and Kings springs in Ash Meadows National Wildlife Refuge, Nye County, Nevada (La Rivers 1953) and this was the first aquatic insect species to be protected under the ESA, where it

Table 1 Aquatic or semiaquatic insect species currently protected or proposed as candidates for protection under the US Endangered Species Act

Common name (USFWS)	Order	Family	Species	Status under US ESA (yr. Protected)	Restricted to springs (cold or warm)?	Geographic distribution
Hine's Emerald Dragonfly	Odonata	Corduliidae	*Somatochlora hineana* Williamson	Endangered (1995)	Yes (cold)	IL, MI, MO, WI
Blackline Hawaiian Damselfly	Odonata	Coenagrionidae	*Megalagrion nigrohamatum nigrolineatum* (Perkins)	Candidate	No	HI
Crimson Hawaiian Damselfly	Odonata	Coenagrionidae	*Megalagrion leptodemus* (Perkins)	Candidate	No	HI
Flying Earwig Hawaiian Damselfly[a]	Odonata	Coenagrionidae	*Megalagrion nesiotes* (Perkins)	Candidate	No	HI
Oceanic Hawaiian Damselfly	Odonata	Coenagrionidae	*Megalagrion oceanicum* McLachlan	Candidate	No	HI
Orangeblack Hawaiian Damselfly	Odonata	Coenagrionidae	*Megalagrion xanthomelas* (Seyls-Longchamps)	Candidate	No	HI
Pacific Hawaiian Damselfly	Odonata	Coenagrionidae	*Megalagrion pacificum* McLachlan	Candidate	No	HI
Ash Meadows Naucorid Bug	Heteroptera	Naucoridae	*Ambrysus amargosus* La Rivers	Threatened (1985)	Yes (warm)	NV
Nevares Spring Naucorid Bug	Heteroptera	Naucoridae	*Ambrysus funebris* La Rivers	Candidate	Yes (warm)	NV
Sequatchie Caddisfly	Trichoptera	Limnephilidae	*Glyphopsyche sequatchie* Etnier and Hix	Candidate	Yes (cold)	TN
Comal Springs Dryopid Beetle	Coleoptera	Dryopidae	*Stygoparnus comalensis* Barr and Spangler	Endangered (1997)	Yes (warm)	TX
Comal Springs Riffle Beetle	Coleoptera	Elmidae	*Heterelmis comalensis* Bosse, Tuff and Brown	Endangered (1997)	Yes (warm)	TX
Stephan's Riffle Beetle	Coleoptera	Elmidae	*Heterelmis stephani* Brown	Candidate	Yes (cold)	AZ
Warm Springs Zaitzevian Riffle Beetle	Coleoptera	Elmidae	*Zaitzevia thermae* (Hatch)	Candidate	Yes (warm)	MT
Hungerford's Crawling Water Beetle	Coleoptera	Haliplidae	*Brychius hungerfordi* Spangler	Endangered (1994)	No	MI, ON

[a] Immature stages of this damselfly have not been reported and may inhabit the terrestrial environment

remains listed as threatened (Polhemus 1993). *Ambrysus funebris* La Rivers is restricted to the Nevares-Travertine Spring complex in Death Valley National Park, Inyo County, California (La Rivers 1949), and was introduced at the nearby Texas Spring and is listed as a candidate for protection. A third species, *A. relictus* Polhemus and Polhemus, was most recently described (Polhemus and Polhemus 1994) and is restricted to five springs within a closed basin in Ash Meadows National Wildlife Refuge in close proximity to *A. amargosus*. In addition to these endemic insects, the ecological communities supported by each of the thermal spring systems they inhabit are highly diverse and endemic. For example, the Ash Meadows National Wildlife Refuge contains 25 endemic animals and plants, which is the highest known endemicity of any locality in the continental United States. Within the Nevares-Travertine Spring complex (Death Valley), several endemic aquatic invertebrates occurring syntopically with *A. funebris* include the Furnace Creek riffle beetle (*Microcylloepus formicoideus* Shepard), three undescribed ostracods (2 *Candona* spp.; 1 *Darwinula* sp.), the Texas Spring amphipod (*Hyalella muerta* Baldinger), the Travertine Springs amphipod (*Hyalella sandra* Baldinger), Badwater snail (*Assiminea infima* Berry), and robust inobius springsnail (*Inobius robustus* Hershler).

The desert spring systems inhabited by the three endemic species of *Ambrysus* are threatened by human disturbance (Williams et al. 1985; Polhemus 1993; Myers and Resh 1999; Sada 2001). These particular naucorids rely on the presence of riffles in the spring outflows for critical habitat (La Rivers 1949, 1953; Polhemus and Polhemus 1994). The microhabitat requirements of a congener in Texas, *A. circumcinctus* Montandon, have been studied in detail, and mean current speed and substratum rock size explained a large portion of the variation in population density (Sites and Willig 1991). When describing *A. funebris* adults, La Rivers (1949) noted that the species was present only in areas of intermediate flow along a 100 yard stretch of Cow (Furnace) Creek, and specifically where the spring outflow was fast enough to remove silt from the substrate, but not forceful enough to remove the coarse gravel.

A recent USFWS survey indicated that *A. funebris* was the rarest of the endemic invertebrates in the highly disturbed Cow (Furnace) Creek (Federal Register 2004), and the species is presently a candidate for protection under the ESA and the only such invertebrate within the spring complex currently being considered for protection. Water originating from the Nevares-Travertine Spring complex (including Cow/Furnace Creek) is diverted at eight locations as a source of potable water for commercial and domestic use (including golf course irrigation), and introduced fish may also pose a threat (Federal Register 2004). Thus, of the three endemic Amargosa River naucorids, *A. funebris* may be the most critically threatened with extinction.

The ability to identify all life stages of threatened species is critical to effective management and key to their use as potential flagship species. The adults (La Rivers 1949) and egg stage (Sites and Nichols 1999) of *A. funebris* have been described previously, but the five nymphal instars remain undescribed. Variation in body size and shape allows effective discrimination of species among genera of Naucoridae (Sites and Willig 1994a), among species of *Ambrysus* (Sites and Willig 1994b) and among populations of conspecific *Ambrysus* from differing thermal environments (Sites et al. 1996). Thus, we present here illustrated descriptions of the five post-embryonic immature stages of *A. funebris*, which will enable: (1) identification of all life stages of this threatened insect species, and (2) comparisons in ontogeny across *Ambrysus* species. Using this example from Death Valley National Park, we argue that aquatic invertebrates may also be effective as umbrella species for aquatic ecosystem protection given their dependence on intact watersheds, the ease with which they can be sampled and their ubiquity even in relatively remote habitats such as continental deserts and oceanic islands.

We also present a list of all aquatic insect taxa in the USA currently protected under the ESA or those listed as candidates (Table 1). Such species are potentially umbrella species for the aquatic ecosystems in which they reside. Additionally, we present a list of aquatic and semi-aquatic Heteroptera that should be considered for protection based primarily on their restricted ranges (Polhemus and Polhemus 2002).

Materials and methods

Ambrysus funebris

Under supervision of Death Valley National Park personnel, we collected samples of *A. funebris* in fast water by kick-sampling within the rocky substratum of Cow (Furnace) Creek upstream from an aquatic D-net (approximate coordinates: 36°24′00″ N, 116°52′34″ W). Samples were collected on 18 August 1990 by Nichols (in ‘‘Furnace Creek’’) and on 2 August 2000 (1.5 miles east of Furnace Creek Inn in the spring which runs parallel to the road) by Whiteman and Whiteman. All specimens were stored in 70% or 100% ethanol. Specimens were brought to the laboratory and discrete size variation among instars allowed us to sort the individuals into five groups. An ocular micrometer was used in all measurements and averages were calculated within each instar for each measurement (Table A2). Body length was measured from the tip of the labrum to the tip of the abdomen and body width was measured as the widest span across the nota. Widths of all other notal sclerites were measured across the midline; synthlipsis was measured as the minimum interocular distance (anteriorly); all leg lengths were maxima (chords for curved structures). Voucher specimens have been deposited in the Enns Entomology Museum, University of Missouri-Columbia.

As a data reduction tool, we used Principal Components Analysis (PCA) in SPSS version 9.0 to describe differences in morphology among instars. Metrics were first transformed using the formula ln*(x + 1) to meet the assumptions of normality. Components with eigenvalues >1 were retained and rotated using varimax. Regression factors (Appendix Table A1) were extracted and plotted against each instar (1–5).

Species of aquatic or semi-aquatic Heteroptera in the USA with restricted ranges were documented by Henry and Froeschner (1988) and Polhemus and Polhemus (2002). We also used the Species Information webpage of the US Fish and Wildlife Service as a source of species that are protected or are candidates for protection under the ESA (http://www.fws.gov/endangered).

Results

Collections and descriptions of nymphal stages of *A. funebris*

All five nymphal instars and adults of *A. funebris* were successfully collected from the same region of Furnace Creek in 2000 (Fig. 1) and all but the second instar were collected in August 1990.

No other naucorids were collected or have been reported from this spring complex. The lack of fully developed hemelytra in the nymphs readily distinguishes them from adults. Differences among nymphal instars were discrete based on either morphometry (Table A2; Fig. 2) or relative extent and pattern of maculation and shape of the nota (Table A2; Appendix Fig. A1). The first principal component explained 97.88% of the variance of the set of variables listed in Table 1 and is considered to be the component based on body size (Sites and Nichols 1990). Body size increased in a linear fashion across molts (Fig. 2), consistent with the pattern within congeners (Sites et al. 1996). Although habitat water temperature is inversely related to body size across *Ambrysus* populations and species (Sites et al. 1996), the water temperatures in the habitat of *A. funebris* are relatively constant (35–40°C; La Rivers 1949). Thus, if individuals of *A. funebris* are collected from its native habitat, the average metrics presented in Table 1 should reliably allow instar assignment of an *A. funebris* nymph. However, if *A. funebris* was reared at temperatures that differed from those in the Nevares-Travertine Spring Complex, differences are expected in the size of each instar. Specifically, warmer temperatures may yield smaller, and cooler temperatures larger, individuals of each nymphal instar and adult stages (Sites et al. 1996; Sites and Willig 2000).

Following Sites and Nichols (1990), the first instar of *A. funebris* is described in detail and only changes in morphology in subsequent instars are noted (see Appendix for descriptions). Although intra-instar variation in overall coloration and maculation pattern on the dorsum exists, we attempted to capture this variation in the illustrations (Appendix Fig. A1a–f).

Four aquatic insects species are currently listed as endangered or threatened under the ESA and 11 aquatic insects are currently listed as candidates for listing under the ESA (Table 1). Of these, eight are restricted to springs or spring outflows. An additional 11 species of Heteroptera

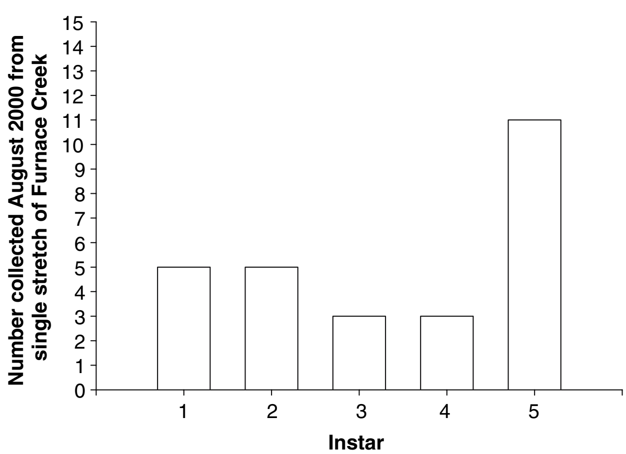

Fig. 1 Distribution in abundance of each instar of *A. funebris* during kick-sampling in Furnace Creek in August 2000

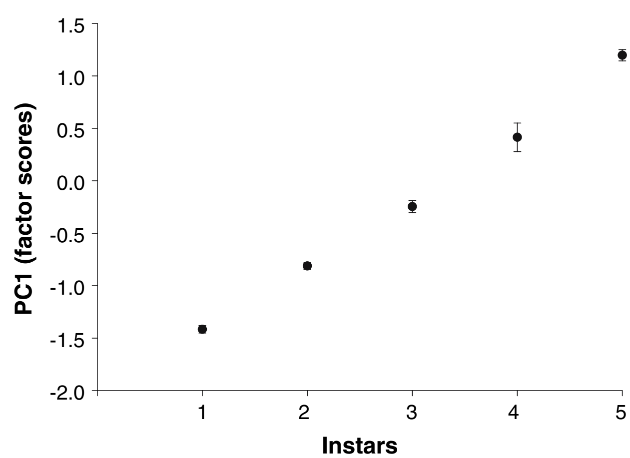

Fig. 2 Ontogenetic variation in size (PC1) of *A. funebris* nymphs. Analyses were conducted on 35 nymph individuals for which complete morphometric data were available

had restricted ranges but were not listed under the ESA or proposed as candidates for protection.

Discussion

Conservation of *Ambrysus funebris* and its potential as an umbrella species for the Furnace Creek ecosystem

The data presented here suggest that in the year 2000, *A. funebris* was reproducing in Furnace Creek and all instars occurred in the same stretch of gravel substrate. The most abundant instar was the fifth, while the third and fourth were the least abundant. Given the relatively high temperatures of Furnace Creek, this species may have the potential to produce three to four generations/year (based on Sites and Nichols 1990), and likely feeds on amphipods (Polhemus and Polhemus 1994). The future of *A. funebris* depends on effective management by the National Park Service of its only native habitat, which is also a primary source of potable water for National Park operations and human use within Death Valley. The 30-year-old water collection system along its course is presently being proposed for removal (Federal Register 2005). During a period in 1999 in which water collection temporarily ceased, water flow was restored to 7 miles of stream habitat along the Furnace Creek wash, demonstrating the severely negative impact that continued water diversion has had on the riparian habitat (Threloff and Koenig 1999). In place of the old water collection system, the 'agency preferred' alternative would install several groundwater wells in the Texas Springs Syncline, allowing the riparian waters associated with Texas and Travertine springs to be released, restoring much of the historic riparian habitat of Furnace Creek. Construction on the new water collection system could begin in 2007 (Federal Register 2005). This would very likely provide more extensive and higher quality habitat to *A. funebris* and the other endemic aquatic invertebrates than is presently available. We recommend that non-native fish be removed and continued surveillance for crayfish and other non-native species should be prioritized. Non-native vegetation should continue to be removed from the banks of the outflows and from the channel to ensure that sunlight reaches the substrate (see Polhemus and Polhemus 1988) as well as to ensure that water flows at an appropriate speed; native plants should continue to be planted in patches along the outflows to maximize diversity of habitats and variation of sunlight intensity along the outflows. Notably, an artificial and gravel-filled concrete flume carrying water from Furnace Creek under California State Highway 1-90, provides good habitat for *A. funebris* (US Fish and Wildlife Service 1990). Water flow should maximize the amount of coarse gravel (if additional gravel is deposited in the channel, extreme care should be taken to ensure particle size is identical to that of existing gravel—see Sites and Willig 1991), which is the preferred habitat of *A. funebris* (La Rivers 1948) and many other species of *Ambrysus* (Sites and Willig 1991; Herrmann et al. 1993), and is also the likely site of oviposition (Usinger 1946). Such simple measures brought another Amargosa naucorid, *A. amargosus*, back from the brink of extinction (Fraser and Martinez 2002). Finally, *A. funebris*, first listed as a candidate species for protection in 2004, should be formally protected under the ESA given that its relative abundance has declined since La Rivers' (1948) first collections, likely due to habitat degradation from water diversion and introduction of non-native species. Since it is the only invertebrate currently listed as a candidate for protection under the ESA from this spring complex, and there are no endemic vertebrates within Furnace Creek, which may ostensibly be more charismatic, its formal protection would render it an umbrella species (Frankel and Soulé 1981), potentially ensuring the protection of the entire aquatic ecosystem within Furnace Creek and associated springs, including the eight other endemic but unprotected (at the federal level) invertebrates.

Although several technical reports relating to the relative abundance and conservation status of *A. funebris* exist, none has been published in the primary scientific literature. Such publications would increase awareness of this species and ecosystem within the scientific community, and likely with the public at large. Published results of these studies would also increase our knowledge of the natural history, ecology and evolution of spring endemics generally (Williams 1991).

There are several important caveats to the use of *A. funebris*, and taxa with similar life histories, as an umbrella species. Because this species cannot disperse by flight and spends its entire life cycle within the water column, protection of similarly flightless taxa [e.g. *Limnocoris moapensis* (La Rivers) at Moapa Warm Springs] may not ensure protection of adult stages of other co-occurring, but more vagile aquatic insects at other sites, such as trichopterans and ephemeropterans, which disperse by flight from the water. Thus, at other sites, volant taxa that rely on an intact riparian zone may be more effective candidates as umbrella species because the water column and associated terrestrial habitat would be protected. Furthermore, each oasis harbors a unique fauna and unique hydrological characteristics, which requires that these oases be considered on a case-by-case basis.

Conservation of endemic Heteroptera in the western US

The arid southwestern United States harbors a number of highly endemic aquatic heteropterans (Polhemus and

Polhemus 1988, 2002). In their biogeographic analysis of aquatic Hemiptera in the Great Basin, Polhemus and Polhemus (2002) noted that a ''most remarkable'' concentration of isolated (disjunct) populations or endemic species of aquatic heteropterans occurs within three river drainages within the warm, southern basins of Nevada and California: Railroad Valley, White River and Amargosa River. Indeed, many of the endemic taxa and disjunct populations residing within the Great Basin are found in these thermal spring systems of the south and few are found in the cold-water systems of the north (Polhemus and Polhemus 2002). In many cases, populations of conspecifics or congeners of many of these species are found in Texas or Mexico, a pattern also found in spring fishes (Polhemus and Polhemus 2002). Using all available information, we provide a list of aquatic heteropteran taxa or populations (named or unnamed) that by virtue of their restricted ranges might be considered further for federal protection (Table 2). All taxa in Table 2 are currently unprotected by federal law and many are restricted to isolated desert springs. We propose that those taxa or highly disjunct populations endemic to a single spring or spring complex should be given high priority for federal protection under the US ESA, including: *Ambrysus funebris* and *A. relictus* (Naucoridae), *Limnocoris moapensis* (La Rivers) (Naucoridae), *Ranatra montezuma* Polhemus (Nepidae), *Ioscytus beameri* (Hodgden) (Saldidae), *Pentacora saratogae* (Cobben) (Saldidae), *Saldula usingeri* Polhemus (Saldidae) and *Rhagovevlia becki* (Veliidae). Notably, many of these species inhabit springs or associated outflows that are all or partially within US federal lands. Thus, listing of these species is unlikely to involve issues relating to private property rights, although the aquifers feeding these springs may be affected by land-use elsewhere. The case of *Ioscytus beamieri* is more worrysome, as it is known only from the type series collected from Las Cruces, New Mexico (Schuh and Slater 1995). An effort should be made to determine if populations of this species still exist. Two naucorid taxa listed are subspecies of *A. mormon*, the most widespread species of *Ambrysus* in the United States. Relatively cryptic morphological variation present in many *A. mormon* and

Table 2 Aquatic or semiaquatic Heteroptera species or subspecies with restricted ranges in the western United States not presently protected or listed as candidates under the US Endangered Species Act

Family	Species	Priority for ESA candidacy	Geographic distribution
Belostomatidae	*Abedus herberti utahensis* (Menke 1960)	Low	UT and AZ: Virgin River drainage
Naucoridae	*Ambrysus mormon heidemanni* (Sites and Willig 2000)	Low	WY: Yellowstone National Park (thermal waters including the Firehole River)
	Ambrysus mormon minor (La Rivers 1963; Sites and Willig 2000)	Low	ID: Owyee Co., Hot Creek (thermal waters), Snake River Drainage
	Ambrysus relictus (Polhemus and Polhemus 1994)	High	NV: Nye Co., Ash Meadows National Wildlife Refuge (thermal waters), Amargosa River Basin
	Limnocoris moapensis (La Rivers 1950b; Sites and Willig 1994a, b)	High	NV: Clark Co., Warm Springs, Moapa River (thermal waters), White River Basin
	Pelocoris biimpressus shoshone (La Rivers 1948; Polhemus and Sites 1995)	Low	CA: Inyo Co., Grapevine Springs, Death Valley National Park (thermal waters)
			NV: Clark Co., Moapa Warm Spring and Blue Point Spring; Nye Co., Railroad Valley, Duckwater, Big and Little Warm Springs; Lincoln Co., Ash Warm Springs (thermal waters), Railroad River Basin, White River Basin, Amargosa River Basin
Nepidae	*Ranatra montezuma* (Sites and Polhemus 1994)	High	AZ: Yavapai Co., Montezuma Well (limestone sink)
Saldidae	*Ioscytus beamieri* (Hodgden 1949)	High	NM: Las Cruces
	Pentacora saratogae (Cobben 1965)	High	CA: Inyo Co., Saratoga Springs, Death Valley National Park, Amargosa River Basin
	Saldula luctuosa (Stål 1859)	Low	CA: Coastal marshes from La Jolla to Tomales Bay
	Saldula usingeri (Polhemus 1967)	High	CA: Colusa Co., nr. Wilbur Hot Springs and Sulphur Creek
Veliidae	*Rhagovelia becki* (Drake and Harris 1936)	High	NV: Clark Co., Moapa Warm Spring (a thermal disjunct from the primary distribution in Texas and Mexcio; Polhemus and Polhemus 2002), White River Basin

Drainage basins after Polhemus and Polhemus (2002)

A. woodburyi populations may indicate that these populations are genetically isolated (Sites and Willig 2000; Polhemus and Polhemus 2002). Future work should focus on determining the phylogeny of the US species of *Ambrysus* as well as conducting comparative population genetics among isolated populations of widespread *Ambrysus* species such as *A. mormon*, and *A. woodburyi* to identify conservation management units (Polhemus and Polhemus 2002; Hurt and Hedrick 2004; Marten et al. 2006). However, results from the single population genetic study of *Ambrysus* to date revealed little genetic differentiation among *A. thermarum* La Rivers populations inhabiting proximal streams in the White Mountains of Arizona (Miller et al. 2002). Nonetheless, the desert Southwest, and in particular the southern Great Basin, has produced a myriad of endemic invertebrate species all reliant on the threatened desert oases in which they reside (Myers and Resh 1999). Such species have the potential to serve as umbrellas for ecosystem protection in this region and elsewhere.

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Appendix 1: Descriptions of immature stages of *Ambrysus funebris*

First Instar (Fig. A1a). Length, 1.91 ± 0.07 mm; width, 1.11 ± 0.05. Body ovoid, highly dorso-ventrally flattened, greatest width at metathorax, greatest length at midline; dorsal coloration light brown, with fine, sparse, irregular punctations light brown in center with dark brown edges throughout; fine setae of variable length covering lateral margin of most of body and posterior margin of abdomen.

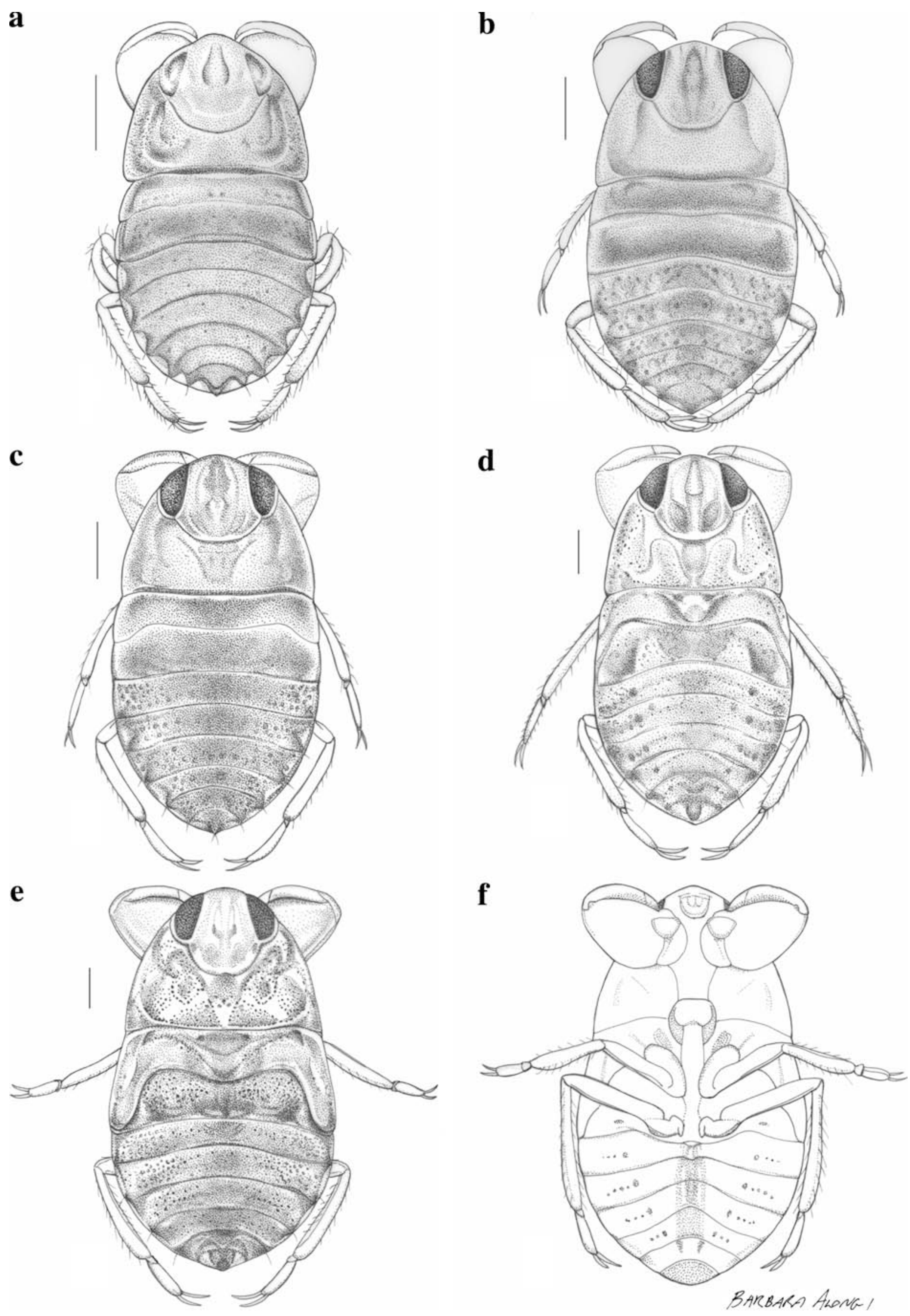
Dorsum of head light brown; straw-yellow ventrally; roughly pentagonal; anterior margin convex, continuous with lateral margins of prothorax; posterior margin lobate and deeply convex; forks of ecdysial cleavage line parallel posterior margin of head and anterior margin of pronotum, which are contiguous; compound eye red (although in some specimens compound eyes were not completely pigmented, but ommatidia were apparent); synthlipsis about 1.5× width of one compound eye; ocelli absent. Antenna light brown, 3-segmented, segment 2 about 2× length of segment 1 and about 0.7× length of segment 3. Beak light brown, elongate-conical, 3-segmented, overall length (with stylets retracted) about 1.2× width at base, segment 2 about 1.5 times length of segment 1 and subequal to length of segment 3.

Mid-dorsal longitudinal suture from anterior margin of pronotum to posterior margin of metanotum. Anterior margin of pronotum deeply concave; posterior margin slightly, evenly convex. Mesonotum apparently shortest of nota; anterior margin subducts beneath pronotum; posterior margin of mesonotum and anterior margin of metanotum subtly sinuate near midline; mesonotal wing-pads only slightly apparent. Metanotum posterior margin broadly concave; overlapping abdominal tergites I and part of II.

Prothoracic leg retentorial (Sites and Nichols 1990), coxa, trochanter light brown, leg otherwise straw-yellow, darkening to amber around margin of profemur and near distal end of protarsus. Procoxa about 3× length of trochanter and about 0.5× length of femur. Profemur laterally compressed; 2 rows of amber pegs directed ventrolaterally and ventromedially, gradually shortening distally, distal pegs about 1/6 length of basal pegs. Protibia with slight sulcus along length of ventral surface. Protarsus 1-segmented with single claw.

Meso- and metathoracic legs straw-yellow, darkening to amber around margins of segments. Mesocoxa ovoid, about 3× length of trochanter and subequal to length of femur. Mesofemur with 2 rows of sharp, amber pegs along entire posterior margin, 1 row along basal 2/3 of anterior margin. Mesotibia with 4 rows of stout, reddish and yellow spines, 2 ventral, 1 lateral and 1 medial; rows sometimes converging distally. Mesotarsus 2-segmented with first segment 1/4× length of second and lobed 2/3 of its length under second; segment 2 with 2 rows of spines, 1 ventral, 1 medial; terminating in paired claws equal in size and about 1/3 length of tarsus. Metacoxa and trochanter resembling those in mesothoracic leg in shape and proportions. Metatibia with four rows of stout reddish spines in arranged in same fashion (''four corners'' of tibia *sensu* La Rivers 1949). Metafemur with pegs along basal 2/3 of posterior margin. Metatarsus 2-segmented with first segment 0.1× length of second segment; 2 rows of spines ventrally along second segment. Natatorial hairs sparse on mesotibia and mesotarsus, dense on metatibia and metatarsus.

Abdomen dorsally light brown with fine, sparse punctuations; lateral edges of tergites translucent; some brown maculation ventrally, with fine setae on sternites; spiracles 1/3 distance from lateral margins to midline on segments I–VIII; spiracle on segment I concealed by metacoxa. Abdominal midline with posterior knob-like tubercle on sternites II–IV and absent from subsequent sternites. Paired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BARBARA ALONG I

◀**Fig. A1** Instars of *A. funebris*. (**a**) Dorsal aspect of first instar. (**b**) Dorsal aspect of second instar. (**c**) Dorsal aspect of third instar. (**d**) Dorsal aspect of fourth instar. (**e**) Dorsal aspect of fifth instar. (**f**) Ventral aspect of fifth instar. Size bars = 0.5 mm

ostioles of dorsal scent glands apparently situated between tergites III and IV, but ostioles actually closed posteriorly by margin of tergite III.

Second Instar (Fig. A1b). Length, 2.63 ± 0.06 mm; width, 1.49 ± 0.07. Greatest body width from metathorax to abdominal segment II. General color of dorsum brown. Brown punctations increasing on meso- and metanotum and abdominal tergites, pronounced near lateral aspects of tergites, notable irregularly bordered brown patches on head and thoracic nota. Whitish patches on lateral aspects of abdominal tergites. Compound eye brownish-red. Segment 2 of antenna about 0.8× length of segment 3 and about 0.3× length of segment 1.

Third Instar (Fig. A1c). Length, 3.36 ± 0.06 mm; width, 1.91 ± 0.05. Patches of dark brown maculations lighter laterally; more maculations ventrally. Pegs on profemur replaced by rows of dense setae. Brown, irregularly bordered maculations cover most of abdomen. Metathoracic wing pads becoming more evident. Tubercles on abdominal sternites II–IV pointed, apices recurving posteriorly. Segment 2 of antenna about 0.6× length of segment 3 and 3× length of segment 1.

Fourth Instar (Fig. A1d). Length, 4.33 ± 0.14 mm; width, 2.50 ± 0.04. Brown maculations more distinct over entire notum. Wing pads larger; length of mesothoracic wing pads laterally about 0.5× length of exposed part of lateral metanotum. Linear, transverse series of brown maculations on each visible abdominal sternite; mid-ventral abdominal pointed tubercles of II–IV replaced by recurving posterior hooks.

Fifth Instar (Figs. A1e, f). Length, 5.54 ± 0.10 mm; width, 3.37 ± 0.10. Mesothoracic wing pad nearly covering metathoracic wing pad, and part of first abdominal tergite at lateral margin. Pilose setation extending along length of ventral abdominal midline from sternite IV to posterior tip of venter.

Table A1 Factor loadings for first principal component

Character	1st PC
Body length	0.997
Body width	0.997
Head length	0.961
Head width	0.997
Synthlipsis	0.985
Pronotal length	0.989
Metanotal length	0.987
Profemur	0.995
Protibia	0.992
Protarsus	0.966
Mesofemur	0.995
Mesotibia	0.991
Mesotarsus	0.991
Metafemur	0.997
Metatibia	0.997
Metatarsus	0.993

Table A2 Descriptive measurements of nymphs of *A. funebris* (in mm ± standard deviation)

Character[a]	1st Instar	2nd Instar	3rd Instar	4th Instar	5th Instar
Body length	1.91 ± 0.07	2.63 ± 0.06	3.36 ± 0.06	4.33 ± 0.14	5.54 ± 0.10
Body width	1.11 ± 0.05	1.49 ± 0.07	1.91 ± 0.05	2.50 ± 0.04	3.37 ± 0.10
Head length	0.47 ± 0.06	0.56 ± 0.02	0.68 ± 0.04	0.79 ± 0.09	0.93 ± 0.08
Head width	0.63 ± 0.02	0.83 ± 0.04	1.02 ± 0.03	1.28 ± 0.04	1.59 ± 0.6
Synthlipsis	0.34 ± 0.01	0.40 ± 0.03	0.49 ± 0.02	0.57 ± 0.03	0.71 ± 0.03
Pronotal length	0.22 ± 0.01	0.34 ± 0.01	0.45 ± 0.03	0.61 ± 0.07	0.77 ± 0.03
Metanotal length	0.25 ± 0.02	0.33 ± 0.01	0.40 ± 0.03	0.49 ± 0.04	0.57 ± 0.02
Leg lengths					
Profemur	0.51 ± 0.01	0.64 ± 0.01	0.77 ± 0.02	1.03 ± 0.04	1.31 ± 0.04
Protibia	0.27 ± 0.02	0.37 ± 0.02	0.48 ± 0.01	0.62 ± 0.01	0.86 ± 0.03
Protarsus	0.18 ± 0.01	0.25 ± 0.01	0.28 ± 0.02	0.30 ± 0.03	0.38 ± 0.02
Mesofemur	0.39 ± 0.02	0.55 ± 0.01	0.71 ± 0.03	0.94 ± 0.05	1.23 ± 0.06
Mesotibia	0.33 ± 0.02	0.48 ± 0.04	0.60 ± 0.03	0.81 ± 0.04	1.12 ± 0.04
Mesotarsus	0.25 ± 0.00	0.37 ± 0.02	0.45 ± 0.04	0.63 ± 0.05	0.75 ± 0.01
Metafemur	0.50 ± 0.00	0.69 ± 0.04	0.88 ± 0.03	1.16 ± 0.05	1.52 ± 0.04
Metatibia	0.50 ± 0.01	0.68 ± 0.03	0.97 ± 0.04	1.29 ± 0.06	1.82 ± 0.06
Metatarsus	0.37 ± 0.03	0.50 ± 0.00	0.63 ± 0.00	0.81 ± 0.08	1.00 ± 0.06

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