Springsnails: A New Conservation Focus in Western North America

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Springsnails (genus Pyrgulopsis*) are one of the most abundant and diverse members of the endemic western North American aquatic biota. These tiny gastropods are imperiled by threats ranging from groundwater pumping to livestock grazing. During the past 25 years, this long-neglected element of biodiversity has emerged as a new focus of conservation-related activities, including protection of several species under the Endangered Species Act and monitoring and habitat restoration efforts. Molecular investigations have helped sharpen springsnail taxonomy and suggest that these animals cannot be managed using a priori assumptions of population structure. Despite this progress, there is an urgent need for additional studies of springsnail natural history, taxonomy, and genetics. The prospects for improving the protection and restoration of springsnail habitats are promising but are clouded by the overarching threat of groundwater mining, which may be addressed best by broader conservation efforts focused on regional groundwater-dependent ecosystems.*

Keywords: biodiversity, conservation, groundwater, western North America, gastropods

Globally, between 10,000 and 20,000 freshwater species are thought to have become extinct or imperiled by human activities (Strayer and Dudgeon 2010). It is estimated that 37% of the world's freshwater species have declined since 1970, which exceeds the trends in terrestrial and marine ecosystems (WWF 2012). Human population growth and global climate change will probably exacerbate threats to freshwater ecosystems and accelerate extinctions in the future. Despite this well-recognized biodiversity crisis, there is a paucity of basic data on the diversity, habitats, and geographic ranges of freshwater species crucial to conservation planning (Abell 2002). This information gap is especially pronounced for invertebrates, which has constrained the opportunities for legal protection of these animals (Strayer 2006).

Efforts to abate declines of freshwater biota in western North America (treated herein as the area west of the Mississippi River) have historically been concentrated on the conservation and management of fishes (e.g., Minckley and Deacon 1991). The hydrobiid gastropod genus *Pyrgulopsis*, composed of 137 western congeners (Hershler et al. 2013), is one of the largest freshwater species radiations in the region. These tiny animals (having 1–8-millimeter-tall shells; figure 1a, 1b; Hershler 1994), commonly known as *springsnails*, are widespread and locally abundant (more than 1000 per square meter; Mladenka and Minshall 2001, Martinez and Sorensen 2007) in suitable habitats throughout much of western North America, which suggests a possibly important role in ecosystem function (e.g., as primary consumers); they are also useful indicators of perennial water sources (e.g., *Pyrgulopsis simplex*; Bogan et al. 2013). (Note that the term *springsnails* has also been applied to several other groups of freshwater gastropods belonging to the superfamily Rissooidea.) Owing to their strong groundwater dependency and typically narrow geographic ranges, often consisting of a single spring or spring complex, springsnails are especially vulnerable to extirpation and extinction in the case of local endemics (Hershler 1998). At least five species have gone extinct since the early 1900s (Hershler 1994, 1998), and the majority of the extant species (104 of 130, 80%) are listed as *endangered* by the American Fisheries Society (Johnson et al. 2013). During the past 25 years, *Pyrgulopsis* has emerged as a new focus of conservation attention in the West, as is evidenced by federal listings and listing petitions, monitoring and recovery actions, and scientific research. The discovery and description of a large number (88) of new *Pyrgulopsis* species during this interval has contributed to a growing appreciation of the biodiversity value of headsprings, and the genus has, on occasion, served as a lightning rod for debate on the competing needs for the declining groundwater resources within the region. However, despite this increasing interest, *Pyrgulopsis* is still poorly known and little studied in most respects, which hampers conservation efforts. Here, we review the recent progress that has been made in better understanding and protecting this long-neglected, species-rich group and discuss the challenges that lie ahead.

The *Pyrgulopsis* radiation

Pyrgulopsis ranges from the Missouri River headwaters south to the Rio Nazas–Rio Aguanaval drainage and from the

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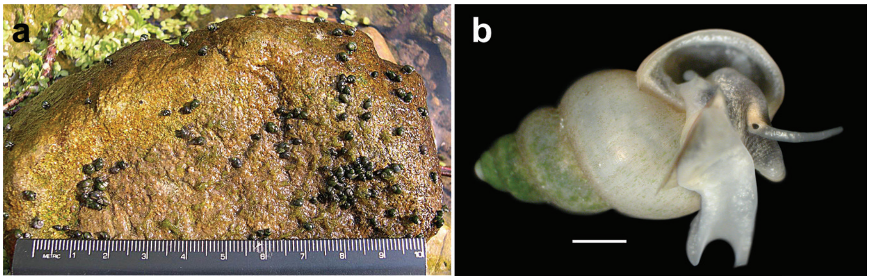

Figure 1. (a) **Pyrgulopsis** *sp. on rock (East Fork Rock Creek, Idaho). Photograph: Daniel Gustafson. (b)* **Pyrgulopsis robusta** *(Snake River, Idaho). The scale bar represents 1 millimeter. Photograph: Robert Hershler.*

lower Rio Grande basin west to the Pacific margin (figure 2). The Great Basin contains the largest number of species (73), followed by the Colorado River basin (29). *Pyrgulopsis* species typically live in seeps and springs (both ambient temperature and thermal) and are often concentrated near sources of groundwater discharge (Hershler 1998). The high fidelity to headsprings in this group may be due, at least in part, to narrow physiological specialization to these habitats (O'Brien and Blinn 1999, Mladenka and Minshall 2001). A few species are also distributed in spring-influenced reaches of rivers or lakes (e.g., *Pyrgulopsis bruneauensis*; USFWS 2007a), and one species ranges into heavily affected reaches of the Snake River, including large reservoirs behind dams (*Pyrgulopsis robusta*; Lysne et al. 2007). A recent microsatellite study (Liu and Hershler 2014) suggests that *P. robusta* may be a polyploid, which provides a possible explanation for its broad environmental tolerance (polyploid vigor) and which suggests a previously unknown facet of the *Pyrgulopsis* radiation (ploidy variation). *Pyrgulopsis* typically lives on emergent macrophytes (e.g., watercress) and hard substrates (Hershler 1998) and grazes on periphyton and attached algae (Mladenka and Minshall 2001, Riley et al. 2008).

Pyrgulopsis species are dioecious, females are oviparous (Hershler 1994), and generation times are short (e.g., 11–14 months, *P. robusta*; Lysne et al. 2007). Recruitment patterns appear to vary according to water temperature (Mladenka and Minshall 2001). Springsnails are gill breathing, have entirely benthic life cycles, and do not tolerate desiccation well. Although dispersal is severely constrained by these traits, there is strong (genetic) evidence that springsnails have been transported across drainage divides by waterbirds on occasion (Liu et al. 2003). However, there are no well-corroborated reports of human activities enhancing springsnail distributions. A recently discovered population at a Montana fish hatchery that was thought to be possibly introduced was subsequently shown to be a new, locally endemic, and genetically divergent species, *Pyrgulopsis blainica* (Hershler et al. 2008).

Systematics, biogeography, and population genetics. The taxonomic inventory of *Pyrgulopsis* is far from complete; numerous putative novelties reported in the literature (e.g., Frest and Johannes 2001) have yet to be formally treated taxonomically, and several large geographic regions have been little explored for these animals (e.g., northwestern Mexico). Taxonomic studies of springsnails have proven to be challenging because of the relatively featureless shells of these animals and the evolutionary convergence (homoplasy) of penial features that are commonly used to diagnose species (Hershler 1994, Liu and Hershler 2005). During the last decade, molecular tools have been used to help resolve springsnail taxonomy (e.g., Hershler et al. 2007, Hershler and Liu 2010). Mitochondrial DNA (mtDNA) analyses have confirmed the distinctiveness of many of the species that were originally described solely on the basis of morphologic criteria (e.g., Hurt 2004) but have also shown that others are cryptic species complexes that require taxonomic revision (e.g., Liu et al. 2003, Liu and Hershler 2007, Hershler and Liu 2010). One of the latter (*Pyrgulopsis micrococcus*) was recently revised and split into four species, three of which were new (Hershler et al. 2013). Molecular data were also used to help delineate a rare case of taxonomic oversplitting of springsnails (*P. robusta*; Hershler and Liu 2004a).

Molecular analyses based on several mitochondrial genes have not well resolved the phylogeny of *Pyrgulopsis* (probably because of rapid diversification of the group or the relatively small number of genetic markers used) but, nonetheless, have shown that the biogeographic history of the group was punctuated by the independent evolution of deeply divergent local species flocks in several parts of the West (Liu and Hershler 2005). These data have also revealed a surprisingly close relationship between *Pyrgulopsis* and *Floridobia*, which is distributed in Atlantic coastal drainage in the eastern United States. Molecular analyses of springsnails have also led to the development of new biogeographic hypotheses for the complex relationships of spring systems in the Cuatro Cienegas Basin (Moline et al. 2004), an ancestral route of the Snake River (Hershler and Liu 2004b) and Pliocene stream capture across the northern continental divide (Hershler et al. 2008).

A rapidly growing literature suggests that most springsnail species are genetically diverse and (when they are distributed among multiple localities) strongly subdivided and that many populations contain private haplotypes (unique mitochondrial DNA sequences; e.g., Hurt 2004). However, the phylogeographic patterns of these animals vary widely, from scant variation across multiple drainage basins (e.g., Hershler and Liu 2004b, Liu and Hershler 2007, Hershler et al. 2013) to strong structure within local spring systems suggestive of incipient allopatric speciation (e.g., several members of the Soldier Meadow species flock; Hershler et al. 2007). An additional pattern is suggested by the occurrence of sympatric-divergent haplotypes in several species,

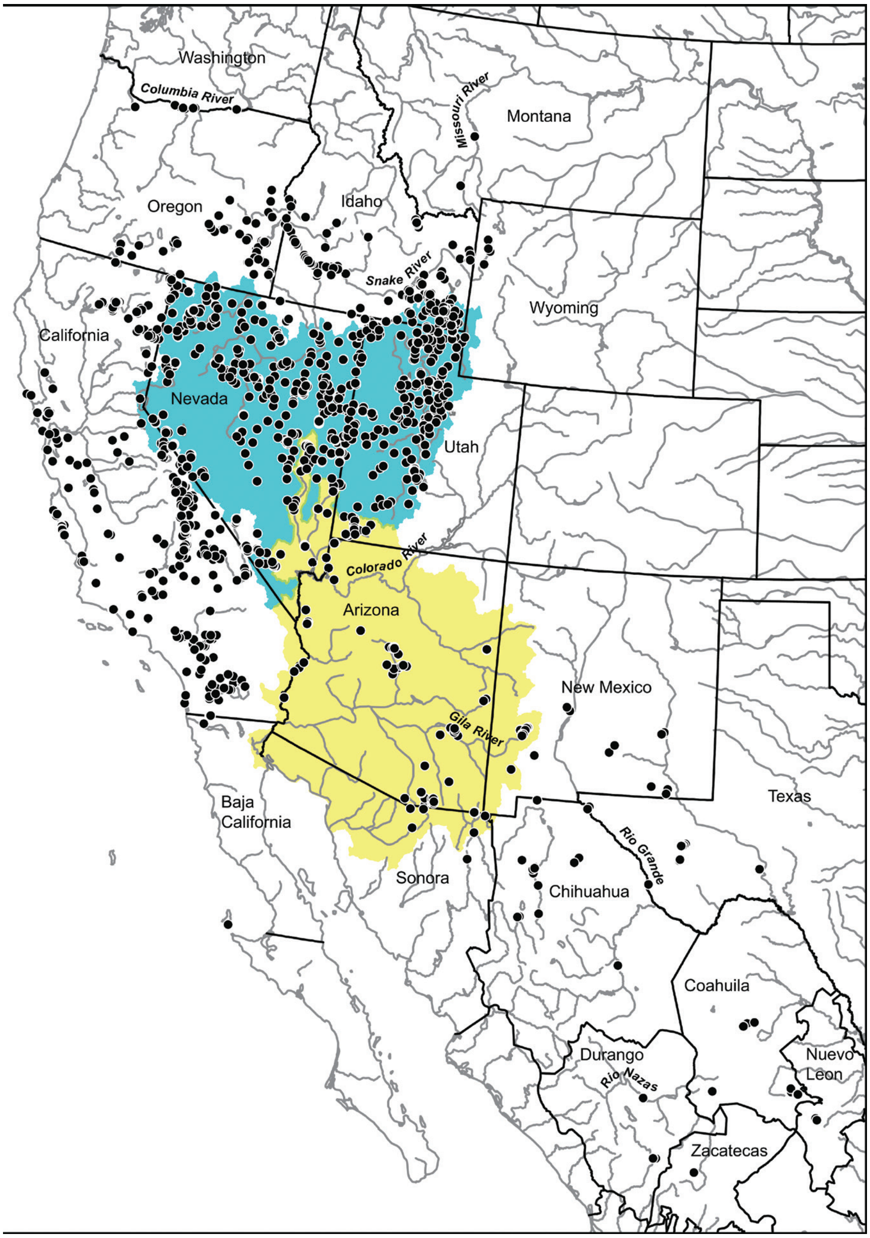

Figure 2. The distribution of* Pyrgulopsis, *based on records in the Smithsonian National Museum of Natural History and several other repositories. The Great Basin and lower Colorado River Basin are shaded in cyan and yellow, respectively.

possibly reflecting admixture (e.g., Hurt 2004, Liu and Hershler 2012).

Threats and status

As a consequence of their strong groundwater dependency, springsnails are vulnerable to both aquifer and surface habitat perturbations. Groundwater pumping and depletion in western North America is occurring rapidly (Aeschbach-Hertig and Gleeson 2012), which has caused the elimination of several springsnail species, including *Pyrgulopsis brandi*, which became extinct in the early 1970s, after the spring complex near Palomas, Chihuahua, (its single locality) dried as a consequence of groundwater pumping (figure 3a; Hershler 1994). The large number of dried springs that are scattered throughout the West (Unmack and Minckley 2008) suggests the likelihood of additional, unrecorded springsnail extinctions. Local populations of several extant springsnails have been extirpated as a result of aquifer drawdown (e.g., *P. bruneauensis*, Myler et al. 2007; *Pyrgulopsis texana*, USFWS 2013). The threat posed by aquifer drawdown is exacerbated in several parts of the West (which are underlain by well-integrated subsurface drainage networks), where local groundwater extraction potentially jeopardizes entire regional faunas (e.g., eastern Great Basin; BLM 2012).

The common practice of capturing and diverting surface flows (e.g., for agricultural or pastoral uses) has also had a devastating impact on springsnail populations (Sada and Vinyard 2002, Abele 2011). In the example shown in figure 3b, a population of *Pyrgulopsis longiglans* became extirpated (between 1993 and 2008) after spring flows were diverted to stock tanks. In cases in which a portion of the groundwater discharge continues to flow onto the landscape, springsnails may persist, albeit in a smaller habitat (figure 3c). *Pyrgulopsis* populations have also been reduced or completely destroyed by impoundments (e.g., *Pyrgulopsis chupaderae*, *Pyrgulopsis neomexicana*; Taylor 1987), channelization of outflows (e.g., *P. texana*, USFWS 2013; various species in Ash Meadows, Hershler and Sada 1987), and other "improvements" to springs. The excavation of Longstreet Spring (Ash Meadows) in the early 1970s to increase discharge (BIO-WEST 2013) probably contributed to the extinction of a putatively undescribed species that was endemic to this locality (the "Longstreet spring snail"; Williams et al. 1985). Additional threats are posed by recreational activities, particularly the extensive use or physical modification of thermal springs for bathing (e.g., Moapa River drainage; Williams et al. 1985).

Livestock (and other large ungulate) grazing, a near-ubiquitous activity in the West, which is often directed toward headspring areas (Springer and Stevens 2009), has also taken a toll on *Pyrgulopsis*. At least one population has been extirpated (*P. chupaderae*, USFWS 2012a), and

Figure 3. (a) Site of (now dried) springs at Las Palomas, Chihuahua, Mexico, formerly occupied by now extinct **Pyrgulopsis brandi**. *The headspring was in the foreground. Photograph: James J. Landye, 24 August 1971. (b) Sevenmile Spring, Winnemucca basin, Nevada. A local population of* **Pyrgulopsis longiglans** *was extirpated at this site after spring flows were diverted to the cattle troughs shown in the photograph. Photograph: Janel Johnson, Nevada Natural Heritage Program, 16 July 2008. (c) Tennessee Spring, Panamint Valley, California. Small (less than 1 square meter) remnant of habitat (watercress) occupied by* **Pyrgulopsis turbatrix** *after the capture of most of the flow in a spring box. Photograph: Robert Hershler, 4 April 1985. (d) Clay Spring, Snake Valley, Utah. Habitat of* **Pyrgulopsis anguina** *degraded by livestock grazing; the snails were restricted to a small area below the headspring. Photograph: Robert Hershler, 9 May 1993. (e) Cement ponds impounding flow from School Springs, Ash Meadows, Nevada. Photograph: Robert Andress, 17 January 2007. (f) Recently renovated spring brook, School Springs. Photograph: Robert Andress, 7 June 2009.*

others have recently declined as a result of trampling, pollution, and other stock impacts (Sada and Vinyard 2002). At many degraded sites, *Pyrgulopsis* persists only in continuously freshened headspring areas (figure 3d; Hershler 1998, Keleher and Rader 2008). Additional threats are posed by invasive species, including two gastropods, *Potamopyrgus antipodarum* (New Zealand mudsnail) and *Melanoides tuberculatus* (red-rimmed melania), which have recently spread across large portions of the West (Brown et al. 2008). Both of these species (primarily) reproduce asexually in their invasive ranges and frequently achieve very high densities at springsnail localities. A recent study showed that the growth rate of *P. robusta* was significantly reduced by the presence of New Zealand mudsnails (Riley et al. 2008). *Pyrgulopsis* also appears to have been negatively affected in various parts of the West by introduced predaceous crayfishes (e.g., Ash Meadows; Hershler and Sada 1987). Several populations of locally endemic *Pyrgulopsis trivialis* are thought to have been extirpated by one of these invaders, *Orconectes virilis* (USFWS 2012b). As a consequence of their limited vagility and narrow environmental tolerances, springsnails may also be vulnerable to the emerging threats associated with climate change (Young et al. 2012).

Conservation

During the past 25 years, considerable strides have been made in providing protection to springsnails. Eight species from the Snake River Basin and the American Southwest (herein treated as Arizona, New Mexico, and western Texas) were added to the federal list of *threatened* and *endangered* species by the US Fish and Wildlife Service (USFWS) between 1991 and 2013; one of these (*Pyrgulopsis idahoensis*) was subsequently delisted (USFWS 2007b) after it was found not to be a distinct species (Hershler and Liu 2004a). Two species from Arizona are federal listing candidates (*Pyrgulopsis morrisoni* and *Pyrgulopsis thompsoni*; USFWS 2012b), and status reviews are currently being conducted for 35 others (from the Great Basin and the American Southwest) to determine whether listing may be warranted (USFWS 2009a, USFWS 2009b, USFWS 2011). Many species are also being afforded some protection because of their distribution in reserves (e.g., Death Valley National Park, 5 species; Ash Meadows National Wildlife Refuge, 7; Cuatro Cienegas Basin, 3). Land was also purchased specifically to help provide protection to springsnails (and other aquatic biota; e.g., Sandia Springs, Texas, and portions of Oasis Valley, Nevada) by The Nature Conservancy in the late 1990s. Many species are also receiving some protection as a result of listings at the state level.

There has also been an increasing amount of on-the-ground springsnail conservation activities during the past two decades. Here, we provide examples from the two principal focal areas of these efforts, the Great Basin and the American Southwest. An extensive field survey of Great Basin springsnails in the 1990s resulted in the description of 58 new species and established a baseline for the conservation status of this fauna (Hershler 1998, Sada and Vinyard 2002). The Nature Conservancy and the Desert Research Institute recently assessed the current condition of a large number of the springsnail localities in Nevada (14 populations were found to have been extirpated), and follow-up actions are planned to reduce threats from livestock grazing and to restore impaired sites (Abele 2011). Each of the seven principal target areas in the Nevada Springs Conservation Plan contains locally endemic springsnail faunas (Abele 2011). Springsnail populations in several basins in eastern Nevada are being closely monitored to assess the possible impacts of proposed groundwater development (of a regional carbonate aquifer) to support the continued growth of Las Vegas (SNWA 2011). Extensively modified springsnail habitats in the Ash Meadows Wildlife Refuge have been restored by the removal of impoundments, the rerouting of discharge into historical flow channels, and the eradication of introduced cichlids and crayfish (Weissenfluh 2010, Scoppettone et al. 2011, BIO-WEST 2013). In the example shown in figure 3e, 3f, School Spring in Ash Meadows (habitat of *Pyrgulopsis pisteri*) was renovated by the removal of concrete ponds (which were constructed in 1983 to expand habitat for pupfish) and the creation of a "naturalized" outflow channel with pools, runs, and riffles (Weissenfluh 2010). In some cases, this work has included heroic (and successful) efforts to salvage and subsequently reintroduce (after habitat restoration) large numbers of *Pyrgulopsis* (Weissenfluh 2010). Recovery work to assist springsnails has also been done elsewhere in southern Nevada (e.g., the removal of impoundments [swimming pools] at the Warm Springs Natural Area; Beck et al. 2006). The Bureau of Land Management implemented various measures to reduce threats to the *Pyrgulopsis* species flock (and other biota) living in local thermal springs in Soldier Meadow (northern Nevada), including the construction of fencing to exclude livestock and other ungulates from the majority of these springs and walkways to direct foot traffic away from these sensitive habitats. *Pyrgulopsis notidicola* was recently removed from the federal candidate list because of these conservation actions (USFWS 2012b).

Springsnails of the American Southwest are being carefully monitored—in some cases, on a monthly basis for more than 10 years (e.g., *Pyrgulopsis roswellensis*; NMDGF 2005)—to assess population trends. Field studies have been carried out to evaluate habitat associations (e.g., *Pyrgulopsis bernardina*; Malcolm et al. 2005) and to estimate population sizes (e.g., *P. morrisoni*; Martinez and Sorensen 2007). There have also been successful efforts to propagate imperiled species in captivity (e.g., *P. morrisoni*; Wells et al. 2012). Restoration activities within the region have included the renovation of springheads (e.g., the removal of structures that prevented sunlight from reaching these habitats) and the construction of fencing to exclude livestock, which improved the status of *P. morrisoni* (a federal candidate species) sufficiently for its threat level to be reduced by the USFWS (2012b); installation of a pump to maintain discharge from Phantom Cave (after this spring failed in the early 2000s) to support habitat for *P. texana* and other biota (USFWS 2013); and drilling of wells to augment flow in one of the few remaining springs occupied by *P. bernardina* (USFWS 2012c).

Conclusions

As was detailed in this brief synopsis, considerable progress has been made recently in the study of springsnails. There are, however, several major knowledge gaps that need to be filled to further facilitate the conservation and management of this large and highly imperiled species radiation; these gaps are discussed below. Also note that although considerable advances have been made in the science of groundwater and the study of groundwater–surface-water interactions over the past few decades, we are still in the early stages of understanding and conserving the epigean species and ecosystems that are reliant on this precious resource (Cantonati et al. 2012). The biogeographic attributes of *Pyrgulopsis*—broad distribution within the West, tight linkage with springs, local endemism of species —suggest that this group can be envisaged as a poster child for these regionally imperiled ecosystems.

There is an acute need for additional investigations of the biology and life history of springsnails to assist conservation efforts. Most of the previous work was done on two species that are at the far ends of the biogeographical spectrum of the group—*P. bruneauensis*, a narrow range thermal endemic, and *P. robusta*, a widely distributed and remarkably tolerant species. Previous ecological studies have, for the most part, consisted of correlative investigations of substrate and habitat usage. Additional experimental investigations are needed to evaluate the role that these locally abundant animals play in benthic food webs, nutrient cycling, and other aspects of ecosystem functioning and to assess their physiological tolerances to relevant environmental parameters to better understand the factors that constrain many species to headsprings. The recent discovery of *P. bruneauensis* in thermal upwellings along the bottom of the Bruneau River (USFWS 2007a) suggests that we may still have much to learn about the use of groundwater habitats by springsnails.

The taxonomic inventory of *Pyrgulopsis* needs to be completed to help direct conservation efforts. Recent descriptions of new springsnails have been followed by rapid conservation action. For example, *Pyrgulopsis castaicensis*, which was described in 2010 from a single spring on southern California lands being developed for (Mission Village) housing (Hershler and Liu 2010), has already been incorporated into the resource management component of this project. The largest taxonomic gaps are the Snake River Basin (Frest and Johannes 2001) and northern Mexico, both of which contain numerous unstudied populations. The need for taxonomic studies of the Mexican *Pyrgulopsis* fauna is especially urgent, given the rapidly declining spring-fed habitats in this region. Note that four of the seven described species from this region recently became extinct (Hershler 1994). As was mentioned above, various springsnail species require taxonomic revision based on mtDNA evidence. The highest priorities of these from the conservation perspective are two widely ranging southern California congeners that may harbor a considerable number of cryptic species (*Pyrgulopsis californiensis*, *Pyrgulopsis stearnsiana*; Hershler and Liu 2010). Given that springsnails tend to be under- rather than oversplit taxonomically, there is also a need for genetic studies of other widely ranging species that have not been previously assayed in this manner to determine whether they may also be composites of multiple taxa (e.g., *Pyrgulopsis gibba*, *Pyrgulopsis kolobensis*; Hershler 1998).

Additional genetic studies are needed to help identify conservation priorities and to guide translocation actions that have been proposed in management and recovery plans. The diversity of patterns revealed by previous phylogeographic studies suggests that springsnails should not be managed on the basis of a priori assumptions of population structure. Many species that are current targets of conservation efforts have not yet been genetically studied in detail (e.g., the majority of the Great Basin fauna) and are, therefore, priorities for these investigations. There is also a need for genetic studies to evaluate the extent to which flow diversions, livestock grazing, and other stressors have increased population fragmentation (e.g., by further constraining snails to headspring areas) and for development of environmental DNA markers to help monitor species. Given that the natural history of most springsnails probably will not be studied in the near future, there is also an urgent need for well-resolved phylogenies, which can be used as tools to infer relevant characteristics for conservation purposes. There is also a need for additional investigations of the impacts of invasive species and for assessments of the utility of some of the conservation measures that are being used—particularly, the fencing of springs to exclude livestock, which can result in the choking of habitat by riparian vegetation that may be deleterious to springsnails (e.g., *Pyrgulopsis bacchus*; Stacey et al. 2011).

There has been a marked upswing in the protection of springsnails during the past 25 years, fueled by strong advocacy from the conservation community. A small number of species are currently protected under the Endangered Species Act (ESA), and many others are being reviewed for possible listing. Conservation actions have been undertaken in many parts of the West with successful results, although there have been some setbacks, including instances in which the current status of federally listed species cannot be assessed because of uncooperative private landowners (*P. chupaderae*, USFWS 2012a; *P. neomexicana*, USFWS 2008). Although this generally promising situation bodes well for the continued protection of the surface habitats of springsnails, the future is clouded by the overarching threat posed by groundwater pumping, which has proven to be intractable and is likely to lead to additional extinctions in the near future because of anticipated increases in water demands (e.g., Arizona fauna; Marshall et al. 2010). The current policies and regulations for groundwater pumping in the West do not adequately involve environmental needs and are, therefore, generally insufficient to protect aquatic biota, even when a federally listed species is nearing extinction, as was noted in the case of *P. bruneauensis* (Myler et al. 2007, USFWS 2007a). Although the purchase of pertinent lands (and the associated water rights) as a means of controlling groundwater development may be a tenable conservation action for a few species, including *P. bruneauensis* (USFWS 2007a), broader protection from this threat will require new sustainability policies that provision water for both humans and aquatic ecosystems (e.g., constraining groundwater extraction to maintain environmental flows). The most fruitful approach for countering this threat may be to integrate and highlight the springsnail agenda into broader and nascent efforts to conserve groundwater-dependent ecosystems (e.g., subterranean aquatic habitats, seeps, springs, spring brooks) in general. The strong advocacy for the conservation of *Pyrgulopsis* (and other spring-dwelling biota) by a diverse group of stakeholders opposing plans for new groundwater mining in eastern Nevada (Schlyer 2007), which has resulted in mitigation measures, ESA petitions, and favorable court rulings, is an encouraging development in this regard.

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